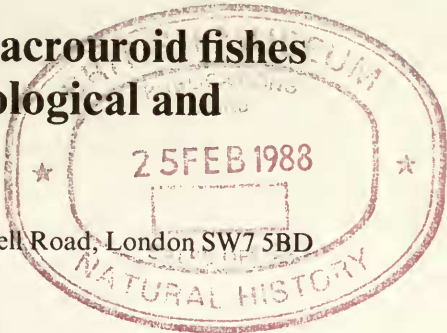


The cranial muscles and ligaments of macrouroid fishes (Teleostei: Gadiformes); functional, ecological and phylogenetic inferences

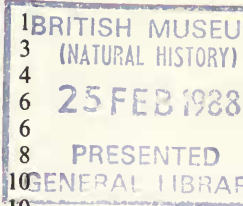
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Introduction

If overall oceanic diversity could be expressed in numbers of individuals and species, rat-tails would surely emerge as the most diverse family of benthopelagic fishes.

So wrote Marshall (1979) of the Macrouridae, a group assigned to that ill-defined assemblage of higher euteleostean fishes known as the Paracanthopterygii.

Marshall (1965) had earlier noted the sparsity of knowledge of the morphology and biology of macrourid fishes. Since then, the studies by Okamura (1970*a* & *b*) have contributed substantially to filling this gap. However, since Okamura studied only Japanese macrourid fishes, the work is taxonomically limited because morphologically more diverse taxa occur outside Japanese waters. The data Okamura has published, nevertheless are substantial enough to provide a foundation for further anatomical studies, particularly those aimed at producing cladistic analyses, which so far, have not been applied to macrourid taxa.

Since Gilbert & Hubbs (1916) published their subfamilial arrangement of macrourid fishes, there have been few major taxonomic changes. Apart from the recognition of additional subfamilies (Parr, 1946) and the elevation of the Macrouroidinae to family level (Okamura, 1970a & b), the most noticeable rearrangement was that of Marshall (1966) who recognised the non-monophyletic nature of the family. Marshall (*op. cit.*) found that three taxa, previously recognised as macrourids, viz: *Steindachneria*, *Lyconus* and *Macruronus*, shared more characters in common with the gadoid family, the Merlucciidae. Although not all of Marshall's chosen characters are synapomorphic for merlucciids, there is every reason to agree that these three genera do not belong with the macrourids (see Cohen, 1984; Howes, 1988).

Most recent authors recognise four macrourid subfamilies (see Cohen, 1984), viz: the Bathygadinae, Trachyrincinae, Macrouroidinae and Macrourinae, the latter containing the majority (*ca* 30) of genera. Howes (1988), based largely on the data presented here, has challenged this concept of the Macrouridae (see below).

Most macrourid taxonomy has been based on ecological-evolutionary premises. For example, Okamura (1970b) viewed his hypothesised phylogenetic polarity of primitive to derived taxa as reflecting both ecological groups and an evolutionary sequence. McLellan (1977: 1034) devised an evolutionary scenario, based on her study of macrourid morphology and ecology, that reflected the invasion of continental slopes and deep ocean basins by taxa derived from pelagic ancestors; again, a sequence supposedly reflected in extant ecological groupings and ontogenetic development.

As pointed out by Marshall (1965; 1979) most macrourids are found in tropical seas but some areas contain more speciose taxa than others, e.g. the Sulu Sea, Gulf of Mexico and Caribbean. Most species are confined to continental slopes and few are common to more than one ocean. Marshall (1973; 1979) has hypothesised that the amphi-Atlantic distribution of 33% of the total Atlantic species and subspecies, might be attributable to continental drift. Merrett *et al.* (1983) also note that species common to the Atlantic and Indian Oceans are inhabitants of continental slope, abyssal and pelagic regions, a distribution seeming to indicate a more general underlying factor than simply one of random dispersal.

In attempting to explain macrourid ecology and distribution, none of these authors has asked a fundamental taxonomic question; how closely related are the taxa under consideration? As yet, there exists no rigorously structured hypothesis of macrourid relationships.

Since previous studies of macrourid morphology have, to a large extent, been concerned with feeding mechanisms and because phylogenetic interpretations have been based on comparisons of those mechanisms, it is the objective of this study to re-assess the morphological basis of those ideas. The jaw musculature of some macrourid taxa has been described by McLellan (1977) and Casinos (1978), these descriptions were, however, made more from a functional rather than a taxonomic and phylogenetic viewpoint, and a taxonomically restricted range of taxa were used. A comparative analysis of macrouroids and other paracanthopterygians would, it was hoped, reveal morphological patterns that might indicate both related groups within the suborder and the relationships of macrouroids with other gadiforms. The limitations of using a single character complex for this purpose are well realised by the author, but past experience with basal euteleosts (Howes, 1984; 1985) has indicated that cranial muscles can provide rewarding information on which to base phylogenetic interpretations.

Where availability of material allowed, at least three specimens of each taxon were dissected to check the variability of the character described.

Okamura (1970b) has described other character complexes (osteology, scales, brain morphology, structure of light organs) and these have been used to a certain extent to test the congruency of relationships arrived at through the myological study. However, these other characters must themselves be evaluated by out-group comparisons, and it is evident in Okamura's analysis that many characters used to define sub-groups are plesiomorphic for Gadiformes. It remains, therefore, for future studies to make polarity assignments to osteological and other characters in order to produce a more refined hypothesis of macrourid interrelationships.

Howes (1988) in an account based principally on the findings presented here has reviewed the relationships of macrouroids and gadoids, and shown that the Macrouroidei (*sensu* Cohen, 1984) and the Macrouridae are non-monophyletic groups. Although, in that previous study, clades were

identified they were not given formal taxonomic status. In this account two of those clades are recognised as families, namely, the Bathygadidae and the Trachyrincidae. More complete diagnoses and taxonomic reviews of both are in preparation. Since the Macroouroidei was restricted to containing a single family the Macrouridae (Howes, 1988), the terms macroroid and macrourid are interchangeable. However, in this text the term macroroid is used when making coordinate comparisons with Gadoidei (*i.e.* gadoids).

Classification used in this text

Suborder: MACROUROIDEI

Family: Macrouridae

Subfamilies: Macrourinae & Macrouroidinae

Suborder: GADOIDEI

Family: Trachyrincidae, Bathygadidae, Moridae, Melanonidae, Steindachneriidae, Eulichthyidae, Merlucciidae, Gadidae, Ranicepitidae, Lotidae, Phycidae, Muraenolepididae & Bregmacerotidae

List of specimens used

All the specimens used in this study are in the collections of the British Museum (Natural History). Type of preparation is indicated as CS = cleared and stained; D = dissected; SK = dry skeleton.

MACROUROIDEI: *Abyssicola macrochir*, 1938.6.23: 12–13 (D); *Cetonurus globiceps*, 1986.4.22: 4–5 (D); *Chalinura mediterranea*, 1986.4.22: 3 (D); *Chalinura profundicula*, 1986.4.22: 9; *Chalinura* cf. *simula*, 1967.12.11: 2 (D); *Coelorinchus caribbaeus*, 1963.2.25: 244–250 (D; CS, 185 mm TL); *Coelorinchus coelorincus*, 1905.2.2: 18 (SK); *Coryphaenoides rupestris*, 1897.12.9: 82 (SK); *Coryphaenoides anguiliceps*, 1981.7.14: 1–4 (D); *Coryphaenoides mexicanus*, 1971.10.22: 24–25 (D); *Cynomacrus piriei*, 1930.1.12: 952; *Echniomacrus mollis*, 1967.12.11: 3–4 (D); *Hymenocephalus italicus*, 1973.3.5: 7–10 (D); *Kumba dentoni*, 1961.1.30: 6 (Holotype; superficial examination); *Lionurus carapinus*, 1934.12.19: 33–34 (D); *Macrosmia phalacra*, 1980.12.31: 2 (Paratype, D); *Macrouroides inflaticeps*, 1939.5.24: 684 (D); *Macrourus berglax*, 1965.6.22: 8–9 (D); *Malacocephalus laevis*, 1960.12.20: 2–3 (D); 1904.11.30: 33 (SK); *Mataeocephalus microstomus*, 1939.5.24: 723–24 (D); *Nematonurus armatus*, 1986.4.22: 1–2 (D); *Nezumia aequalis*, 1973.3.5: 60–64 (CS, 130 mm, tail broken); *Nezumia hildebrandi*, 1963.2.25: 138–153 (D); *Odontomacrus murrayi*, 1967.12.11: 5 (D); *Sphagemacrus hirundo*, 1934.12.19: 30 (D); 1986.4.22: 6–7 (D); *Squalogadus modificatus*, 1963.2.1: 10 (D); *Trachonurus villosus*, 1963.2.25: 226–228 (D); *Ventrifossa occidentalis*, 1965.2.25: 61–71 (D; CS, 190 mm TL).

GADOIDEI: *Antimora rostrata*, 1903.9.29: 7 (D); 1986.4.22: 10–11 (CS); *Austrophycis marginata*, 1936.8.26: 424–431 (D; CS); *Bathygadus favosus*, 1963.2.25: 28–30 (D); *Bathygadus macrops*, 1973.3.5: 3–6 (D); *Bathygadus melanobranchus*, 1969.6.26: 3227–3231 (D, CS); *Bathygadus vaillanti*, 1963.2.2: 31–35 (D); *Bregmaceros atlanticus*, 1984.11.14: 4 (D); *Bregmaceros maclellandi*, 1939.5.24: 792, 799 (D); *Brosme brosmes*, 1892.6.8: 9 (SK); *Ciliata mustela*, 1983.8.3: 13–26 (D); *Enchelyopus cimbrius*, 1980.12.18: 3–12 (D); *Eulichthys polynemus*, 1986.5.14: 1–3; 4–9 (D); *Gadomus longifilis*, 1963.2.25: 7–17 (D; CS, 190 mm TL; 1890.6.16: 43 (SK); *Gadus morhua morhua*, 1971.2.16: 634–635 (D); 1971.2.16: 628–633 (CS, 81 mm SL); *Gadus morhua callaris*, 1985.9.6: 7–14 (D); *Gaidropsarus mediterraneus*, 1971.10.7: 65–77 (D); uncat. (CS, 122, 54 mm SL); *Halargyreus affinis*, 1973.10.29: 384–440 (D; CS, 117 mm TL); *Lepidion eques*, 1981.3.16: 422–427 (D); 11981.3.16: 437–440 (CS, 110 mm TL); 1902.10.30: 6 (SK); *Lota lota*, 1953.6.26: 15–18 (D); 168.6 (SK, skulls only); *Lotilla marginata*, 1974.9.28: 6–7 (CS, 118 mm TL); *Lyconus brachycolus*, 1907.6.20: 15 (Holotype, partly dissected); *Macruronus magellanicus*, 1936.8.26: 352–357 (D); *Macruronus novozelandi*, 25, 120 (SK); *Merlangius merlangus*, 1971.2.16: 329–331 (D); *Melanonus gracilis*, 1930.1.12: 933 (D); *Melanonus zugmayeri*, 1981.3.16: 377 (D); 1986.4.22: 8 (CS, 140 mm TL); *Merluccius merluccius*, 1963.5.14: 94–109 (D); 1971.7.21: 44–57 (CS, 130 mm TL); *Merluccius productus*, 1896.9.25: 6 (SK); *Molva molva*, 1976.6.29: 2–5 (D); *Mora moro*, 25.370 (SK); *Muraenolepis microps*, 1937.7.12: 24–29 (D); 1937.7.12: 11–17 (CS, 95 mm TL); 1937.7.12: 24–29 (skull); *Physiculus argyropastus*, 1901.1.30: 22 (SK); *Phycis blennoides*, 1973.10.29: 4411–448 (D); 1976.7.30: 119 (CS); 1898.4.30: 14 (SK); *Pseudophycis breviusculus*, 1873.12.13: 30 (SK); *Phycis phycis*, 25.400 (SK); *Raniceps raninus* 1967.1.1: 4 (D); 1893.7.6: 2 (D) 1971.2.16: 640 (CS, 40 mm SL); 1864.8.26: 3 (SK); *Salilota australis*, 1936.8.26: 394–404 (CS, 58 mm TL); *Steindachneria argentea*, 1963.2.25: 335–339 (D); 1963.2.25: 344–354 (CS, 130 mm TL); *Trachyrincus trachyrincus*, 1904.11.30: 34–35 (D); 1976.7.30: 42–53 (D, CS, 110 mm TL); 1888.6.15: 7 (SK); *Urophycis regia*, 1985.6.6: 109–119 (D).

OUT-GROUP SPECIES: *Atherina presbyter*, 1983.4.21: 28–37; *Aulopus filamentosus*, 1953.11.1: 10–13; *Brotula jayakari*, 1891.2.9: 30 (SK); *Cataetyx messieri*, 1936.8.26: 1060–61 (D); *Centropomus ensiferus*, 1984.8.8: 85–95 (D); *Cynoscion jamaicensis*, 1961.9.1: 107–113 (D); *Dicrolene introniger*, 1939.5.24: 1441–1444 (D); *Diplacanthopoma brachysoma*, 1972.10.24: 4 (D); *Electrona antarctica*, 1948.5.14: 128–138; *Eleotris obscurus*, 1903.5.14: 93–99 (D); *Esox lucius*, 1971.11.19: 45–46 (D); *Genypterus blacodes*, 1936.8.26: 1052–57 (D); 1898.6.17: 73 (SK); *Glyptothidium macropus*, 1939.5.24: 1456–1465; *Gobiesox nudus*, 1985.3.18: 110–114 (D); *Gobius guineensis*, 1984.7.29: 1021–22 (D); *Harpadon nehereus*, uncat. (D); *Hoplostethes melanopus*, 1939.5.24: 817–8 (D); *Lampanyctus crocodilus*, 1976.7.30: 26–33 (D); *Lamprogrammus niger*, 1939.5.24: 1483–87 (D); *Lophiodes mutilus*, 1939.5.24: 1869–75 (D); *Lycodes frigidus*, 1969.6.26: 3145–49 (D); *Monomitopus metriostoma*, 1964.8.6: 43–46 (D); *Ophidion rochei*, 1971.12.17: 6–8 (D); *Percichthys trucha*, 1981.10.14: 28 (D); *Percopsis omiscomayus*, 1973.3.20: 468 (D); *Photichthys argenteus*, 1930.1.12: 299–306; *Plagioscion squamosissimus*, 1970.4.2: 5–8 (D); *Pogonias chromis*, 1886.1.21: 11–13 (D); *Polymixia nobilis*, 1862.4.22: 17–18 (D); *Porichthys porosissimus*, 1948.8.6: 1460–72 (D); *Serranus cabrilla*, 1960.6.10: 6–8 (D); *Siniperca knerii*, 1981.2.3: 1–4 (D); *Stephanoberyx monae*, 1972.10.24: 2–3; *Tilapia mariae*, uncat. (D).

Abbreviations used in the text figures

NB. Scale bars in all figures are in divisions of 1 mm.

A1, A1 α , A1 β , A1 γ , A2, A2d, A2v, A3, A ω Divisions of the *adductor mandibulae* musculature

Aa	Anguloarticular
aap	<i>adductor arcus palatini</i> muscle
ad	<i>adductores</i> muscle
AH	Anterohyal
bf	buccalis facialis of trigeminal nerve
bpm	bucco-pharyngeal membrane of 1st gill-arch
Bsr	Branchiostegal membrane
Cb	Ceratobranchial
ce	chondroid element
Cmb	Coronomeckelian bone
Cmc	Coronomeckelian cartilage
ct	connective tissue
De	Dentary
Dh	Dorsohyal
do	<i>dilatator operculi</i> muscle
Eb	Epibranchial
Ent	Entopterygoid
epx	<i>epaxialis</i> muscle
ey	eyeball
fA2	fascia of muscle A2
Hb	Hypobranchial
ht	heart
hyab	<i>hyohyoideus abductores</i> muscle
hyad	<i>hyohyoideus adductores</i> muscle
Hyo	Hyomandibula
Hyop	Opercular process of hyomandibula
ica	<i>infracarinalis anterior</i> muscle
iA1 β	internal aponeurosis of muscle A1 β
IO	Interoperculum
im	<i>intermandibularis</i> muscle
lap	<i>levator arcus palatini</i> muscle
le	<i>levator externus</i> muscle
Let	Lateral ethmoid
lcdh	ceratobranchial-dorsohyal ligament
lec	lateral ethmoid-entopterygoid ligament
lei	entopterygoid-infraorbital ligament
lep	lateral ethmoid-palatine ligament
les	lateral ethmoid-suspensorial ligament
li	<i>levator internus</i> muscle
lip	interopercular-preopercular ligament

lla	labial ligament
lmh	mandibulo-hyoid ligament
lmi	mandibulo-interopercular ligament
lmm	maxillo-mandibular ligament
lmn	maxillary-nasal ligament
lmp	maxillary-premaxillary ligament
lmq	mandibulo-quadrate ligament
lo	<i>levator operculi</i> muscle
lpl	palatine-lachrymal ligament
lsm	supramaxillary ligament
lsc	semicircular ligament connecting 3rd hypobranchials
ludh	urohyal-dorsohyal ligament
IVII	maxillary-rostral cartilage ligament
IIX	maxillary-premaxillary ligament
IX	palatine-maxillary ligament
IXI	ethmoid-maxillary ligament
IXII	palatine-premaxillary ligament
Men	Meniscus
Met	Metapterygoid
Mmc	Mentomeckelian cavity
Mvp	Maxillary ventromedial process
Mx	Maxilla
Mxh	Maxillary head
nm	neuromast
NII	Optic nerve
NV	Trigeminal nerve trunk
NVII	Facial (hyomandibularis) nerve
NVIIh	Hyoid branch of facial nerve
NVIIIm	Mandibular branch of facial nerve
obd	<i>obliqui dorsales</i> muscle
obp	<i>obliquus posterior</i> muscle
obs	<i>obliquus superior</i> muscle
obv	<i>obliqui ventrales</i> muscle
oi	<i>obliquus inferior</i> muscle
Op	Operculum
Pal	Palatine
Pb	Pharyngobranchial
pce	<i>pharyngoclavicularis externus</i> muscle
pci	<i>pharyngoclavicularis internus</i> muscle
Ph	Posterohyal
phy	<i>protractor hyoideus</i> muscle
Pmx	Premaxilla
Po	Preoperculum
Pro	Prootic
Ps	Parasphenoid
Pte	Pterotic
Ptt	Posttemporal
Q	Quadrate
Rc	Rostral cartilage
rd	<i>retractor dorsalis</i> muscle
Ra	Retroarticular
Rbv	Buccal branch of trigeminal nerve
rc	<i>rectus communis</i> muscle
rd	<i>retractor dorsalis</i> muscle
re	<i>rectus externus</i> muscle
rei	<i>rectus inferior</i> muscle
ri	<i>rectus internus</i> muscle
RmV	Mandibular branch of trigeminal nerve
RmxV	Maxillary branch of trigeminal nerve

rs	<i>rectus superior</i> muscle
rv	<i>recti ventrales</i> muscle
ScI	Supracleithrum
sh	<i>sternohyoideus</i> muscle
shl	lateral segment of <i>sternohyoideus</i>
So	Suboperculum
Tp	Toothplate
tv	<i>transversus</i> muscle
tvd	<i>transversi dorsalis</i> muscle
tA1 α , t1, t2	insertion tendons of <i>adductor mandibulae</i> A1 muscles
tA2	insertion tendon of <i>adductor mandibulae</i> A2 muscle
Vo	Vomer

Cranial ligaments

Ligaments of the upper jaw and pterygoid bones

In the following account the terminology and numbering system for ligaments follows that of Stiassny (1986).

Stiassny (1986) recognised two synapomorphic arthrological characters uniting the acanthomorph lineages 'Paracanthopterygii' and Acanthopterygii, namely:

- the absence of a median palato-maxillary ligament (ligament IV) and
- the subdivision of the palato-vomerine ligament (ligament VI).

I would confirm Stiassny's findings that a median palato-maxillary ligament (IV) is absent in all paracanthopterygian taxa examined.

In macrouroids there is a single, undivided *palato-vomerine ligament*, which, from its points of attachment to the centre of the palatine and the head of the vomer, corresponds with Stiassny's ligament V (the posterior palato-vomerine ligament). The ligament runs parallel to the medial face of the palatine and varies in size from a long slender strap to a broad band. In the latter case the palatine is deep and is closely applied to the ethmo-vomerine bloc (e.g. *Coryphaenoides*, *Hymenocephalus*).

In Gadoidei the palato-vomerine ligament is also single. The presence of a single rather than a double ligamentous connection in gadoids and macrouroids may indicate that there has either been a derived loss of the anterior palato-vomerine ligament (ligament VI) or that it represents the plesiomorphic condition found in non-acanthomorph fishes. A broad investigation of the condition among paracanthopterygians is necessary to support one or other of these hypotheses.

The *maxillo-rostroroid ligament* (ligament VII) is well-developed in all macrouroids. As in other acanthomorphs it runs from the medial portion of the folded maxillary head to the dorsolateral face of the rostral-cartilage. In all macrouroids ligament VII appears to be continuous across the dorsal surface of the cartilage. In gadoids, a similar situation obtains in *Bathygadus* and the Moridae where the ligament lies in a groove in the cartilage. In many other gadoids, however, ligament VII is broader and inserts on the lateral face of the rostral cartilage (Figs 13 & 17).

In some macrouroids, ligament VII runs parallel to the palato-maxillary ligament (XII), e.g. *Coryphaenoides* (Fig. 1) whereas in others it runs at ca. 45° to that ligament (Fig. 3). Ligament VII passes medial to the tips of the premaxillary ascending processes and is not attached to them. According to Stiassny (1986) in acanthomorphs ligament VII inserts on the premaxillary ascending processes. I have not found this attachment in any gadiform and the condition she reports is probably a derived one for acanthopterygians. Gosline (1981) has commented on the functional significance of ligament VII (Gosline's ligament rc) believing it to be the primary cause of upper jaw protrusion in at least some acanthomorphs (see p. 50).

Casinos (1978) although identifying ligament VII in macrouroids incorrectly states that it is absent in the Gadidae. In fact the ligament is present in all gadoid taxa (see comments on p. 51 concerning function).

An *anterior maxillo-premaxillary ligament* (ligament IX of Stiassny, 1986; ligament 'am' of Gosline, 1981) is present in all macrouroids and other gadiforms examined. In macrouroids

however, the ligaments of either side meet ventroposteriorly to the rostral-cartilage forming an X-shaped ligament connecting the maxillary heads (their menisci) and the premaxillary ascending processes (Figs 28B & C).

In gadoids ligament IX is variously developed and attached. In *Bathygadus* and *Trachyrincus*, there is a complex attachment of the ligament to the maxillary head via a cylindrical chondroid or fibrous element whose posterior tip joins a thin ligament stretching caudally, which becomes incorporated with the connective tissue stretching between the maxilla and premaxilla (Figs 29A & B). In melanonids and merlucciids, ligament IX attaches directly to the medial process of the maxillary head, although it may be associated with a thick wedge of fibrous connective tissue (Fig. 29C). In advanced gadoids, there is sometimes no discrete ligament but only tough connective tissue (e.g. *Euclichthys*) although in the majority there is a short ligament and a thin meniscus between the medial maxillary process and the premaxillary ascending process (Fig. 29D); see further comments on p. 39.

An *anterior palato-maxillary ligament* (ligament X) is present in all macroroids and gadoids examined. It generally connects the base of the palatine prong with the inner central portion of the maxillary head. However, in the macroroids *Coryphaenoides* and *Hymenocephalus*, the ligament attaches to the medial aspect of the maxillary head then passes forward to attach to the anterior process of the premaxilla.

An *ethmo-maxillary ligament* (ligament XI) is well-developed in all macroroids and passes beneath the palato-premaxillary ligament (XII). Its attachments are to the lateral prong of the mesethmoid and the anterolateral face of the maxilla.

In two macrourid genera, *Cetonurus* (Fig. 4) and *Echinomacrus*, a ligament extends transversely from the ethmoid to the palatine. In this respect, the situation corresponds with that in the percomorph *Morone* illustrated by Stiassny (1986, fig. 10). According to Stiassny the additional ligament is a branch of a bifurcated ligament XI. Such may also be the case in the two macrourid taxa. It is noted that in both these genera the dorsal palatine process is higher than in others and that a lateral ethmo-palatine ligament is absent. Thus the 'additional' ligament may serve to brace the palatine against too great a lateral movement.

In all Macrourinae there is a short ligament running from the head of the maxilla to the inner face of the extended nasal bone (Fig. 2). The ligament branches from the base of ligament XI; it is absent in *Bathygadus*, *Gadomus*, *Trachyrincus* and all other gadiform fishes. A maxillary-nasal ligament is apparently present in some acanthopterygians (Cichlidae, P. H. Greenwood, pers. comm.). I have not found the ligament in other paracanthopterygians examined, nor in berycoids or polymixiids.

A *palato-premaxillary ligament* (ligament XII of Stiassny, 1986) is present in all macroroids and runs from the base of the palatine prong to the contralateral premaxillary ascending process. Often, the ligament attaches to the antero-dorsal surface of the rostral cartilage prior to its insertion on the premaxillary process. Gosline (1963, fig. 5A) shows a similar situation in the percopsiform *Aphredoderus* where ligament XII as well as attaching to the rostral cartilage is united with its antimere in the midline. In *Percopsis*, however, the ligament of each side attaches to its respective premaxillary ascending process, there being no contralateral attachment. The percopsiform situation may represent the plesiomorphic condition of ligament XII.

A *lateral ethmoid-palatine ligament* is present in all macroroids examined. This ligament, commonly present in nearly all teleosts, connects the posterior face of the lateral ethmoid wing with the dorsomedial surface of the palatine. In macroroids, there are often two ligaments, the medial occupying the usual position, while the lateral ligament connects the outer margin of the lateral ethmoid to the lateral surface of the palatine. In the macrourines *Nezumia* and *Ventrifossa* the medial ligament extends posteriorly to the entopterygoid. *Cynomacrus* and *Odontomacrus* are exceptional among macroroids in lacking a lateral ethmoid-palatine ligament.

In the gadoid families Melanonidae, Merlucciidae and Steindachneriidae there is a single, stout lateral ligament connecting the lateral ethmoid with the palatine, which in *Gadomus* (Bathygadidae) extends medially to attach to the entopterygoid.

In the Euclichthyidae there is a unique form of ligamentous connection between the lateral ethmoid and suspensorial elements. The lateral ethmoid ligament fans out to attach along the

dorsolateral surface of the palatine; it continues forward as a broad band along the dorsolateral border of the entopterygoid, enters to *adductor arcus palatini* muscle, curves ventrolaterally, leaves the muscle and attaches to the antero-medial face of the hyomandibula (Fig. 15).

In the Moridae there are both separate lateral and medial lateral ethmoid-palatine ligaments, and a lateral ethmoid-entopterygoid ligament. In the Gadidae, however, there are no definite ligamentous connections between the posterior face of the lateral ethmoid and the palatine. In most gadids, the palatine's only ligamentous connection with the neurocranium is with the vomer (ligament V; see above). The lateral ethmoid wing of gadids is often reduced and the palatine articulates not with the wing but with the anterior part of the lateral ethmoid where it contacts the ethmovomerine bloc. In the Muraenolepididae, for example, the palatine bears a high dorsal process which contacts the dorsomedial face of the (considerably reduced) lateral ethmoid. The palatine process is tightly bound by connective tissue to the lateral ethmoid but is not connected to it by a discrete ligament.

Among more 'advanced' gadoids there is a noticeable shift in the articulation of the palatine toward a more anteromedial position. Among macrouroids and plesiomorphic gadoids (Bathygadidae; Melanonidae), the palatine articulates with the ventral surface of the lateral ethmoid wing to which it is also ligamentously attached. In other gadoid taxa, however, the palatine articulates with the anterior, ethmoidal part of the lateral ethmoid and there is a correlated loss of ligamentous connection between the bones. In acanthopterygians, the lateral ethmoid-palatine connection may be *via* one or more ligaments (see for example, Stiassny, 1981: 74; Greenwood, 1985: 158). The widespread occurrence of discrete ligamentous connections between the lateral ethmoid and palatine in teleosts indicates that their absence, often coupled with that of an intimate articulation between the two bones (Howes, 1987) represents a derived condition.

Ligaments of the lower jaw and opercular bones

There is a single, strong mandibular-interopercular ligament present in all macrouroids. The ligament is variable in length and width, from long and strap-like to short and triangular. The mandibular attachment of the ligament is the retroarticular, which is usually dorso-ventrally elongate. Okamura (1970*b*) has drawn attention to the varying types of retroarticular among macrouroids.

Casinos (1978) refers to a 'circumbuccal' ligament in macrouroids and gadids which he describes as a '... tendon that contours all the mouth'. Casinos postulates that this ligament plays an important role in protrusion of the upper jaw (see p. 52). The 'circumbuccal' ligament of Casinos is present in some form or other in all gadiform fishes examined. It does not surround the perimeter of the jaw as is implied by Casinos, but is attached anteriorly to each dentary. I thus refer to it as the 'labial ligament'. The ligament varies in degree of thickness and complexity of anterior attachment, among gadoids being least in the Gadidae and most in the Bathygadidae, Moridae, Melanonidae and Merlucciidae. In macrouroids the ligament is also well-developed, but less so than in the four gadoid families.

In *Bathygadus* (Fig. 9) where it is most highly developed, the labial ligament is a thick rope-like element having a bifurcate attachment on the anterior aspect of the dentary. At the rictus of the jaws, the ligament curves around to attach to the premaxilla, at the point of curvature sending off a posterior branch which anchors to the maxillary rim.

A separate element, with the same gross consistency as the main ligament, forms a stump on the posteromedial surface of the maxilla, rising above the border of the bone. Rosen & Patterson (1969: 425) refer to this non-osseous structure in *Melanonus* (Melanonidae) as resembling a supramaxilla. I therefore refer to it as the 'supramaxillary ligament'.

Histological sections of the labial and supramaxillary ligament, stained specifically for elastin, reveal the 'ligaments' to consist of a collagenous core surrounded by an elastin coat. This tissue is ligament-like in the nature of its attachments (it is free from the dentary, although closely adhering to it by a sheet of connective tissue, which is highly innervated by subbranches of the ramus mandibularis facialis (VII) nerve).

The distribution of the labial ligament among euteleosts is yet to be ascertained but is possibly a

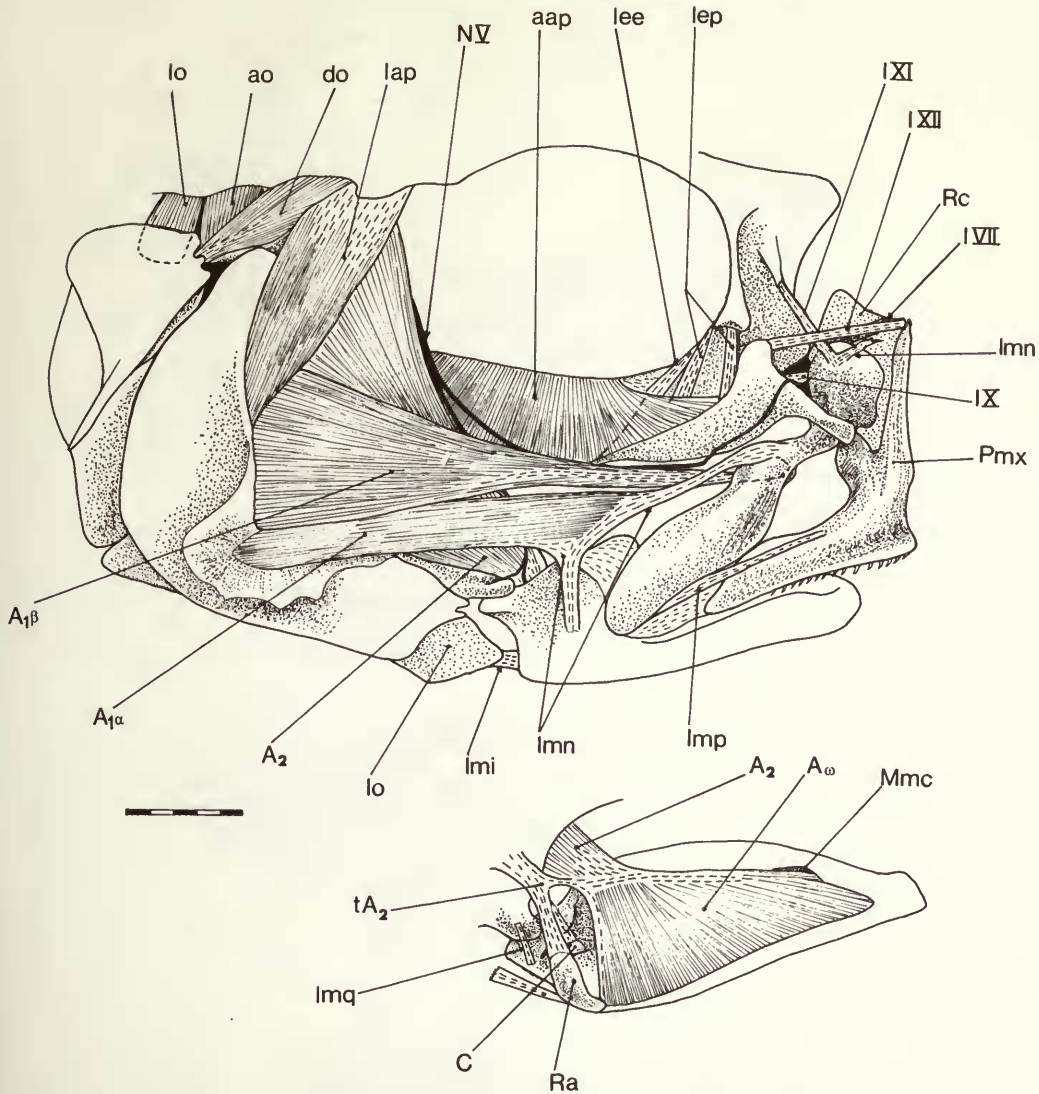


Fig. 1 *Coryphaenoides mexicanus*; cranial muscles and ligaments. Above, in lateral view. Below, medial view of the lower jaw adductor musculature and ligamentous connections.

eurypterygian character (Stiassny, pers. comm.). However, its complex posterior ramification in the gadoids listed above appears to be a derived specialization, whose functional significance is commented upon elsewhere (p. 52).

The ligament which in euteleosts connects the posterior tip of the interoperculum to the anterior border of the suboperculum is, in *Bathygadus* and *Gadomus* reduced and supplemented by another ligament stretching from the dorsal midpoint of the interoperculum to the preoperculum and hyomandibula. In most gadoids the interoperculum and suboperculum are connected by thin connective tissue, the dorsally directed ligament spanning the two bones and attaching to the preoperculum and hyomandibula. In the Merlucciidae, the dorsal ligament is a broad band attaching the interoperculum to the preoperculum. The Trachyrincidae have a unique condition whereby the interoperculum is connected by dorsally directed ligaments to the preoperculum and opercu-

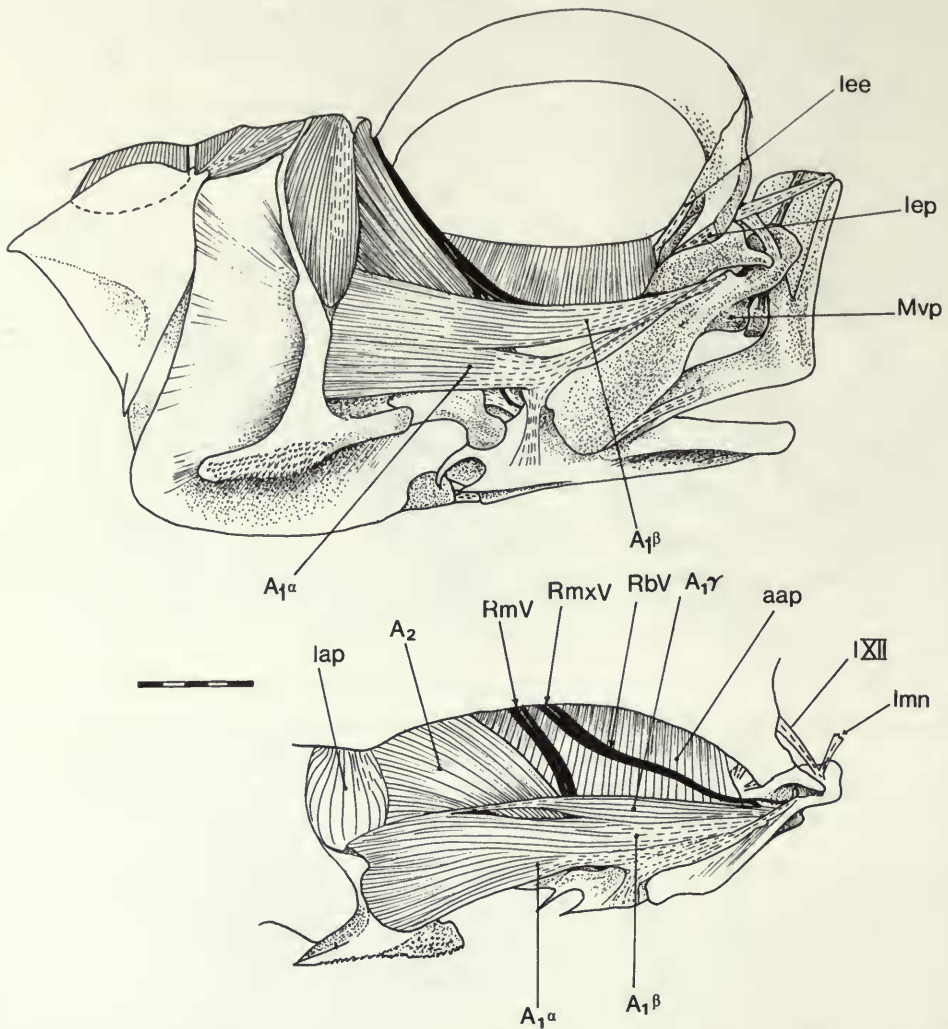


Fig. 2 *Coelorinchus caribbaeus*; cranial muscles and ligaments. In lateral (above) and dorsal (below) views.

lum (see Howes, 1988, figs 2 & 3). The ligamentous connection between the interoperculum and hyomandibula/preoperculum is considered to be a derived condition for gadoid fishes; its taxonomic and phylogenetic implications are discussed more fully in Howes (1988). The functional aspects of this linkage are discussed below, p. 54.

Cranial muscles

The adductor mandibulae and muscles of the suspensorium in macrouroids

The muscles of the jaws and suspensorium in macrourids have been described for some taxa by Dietz, 1921, McLellan, 1977 and Casinos, 1978; 1981. Dietz gave a brief description of the muscles in *Coleorinchus coelorinchus*; McLellan referred to, and illustrated the adductor muscles of *Bathygadus* and *Coelorinchus*, and Casinos those of *Coryphaenoides* and *Trachyrhynchus*. The two

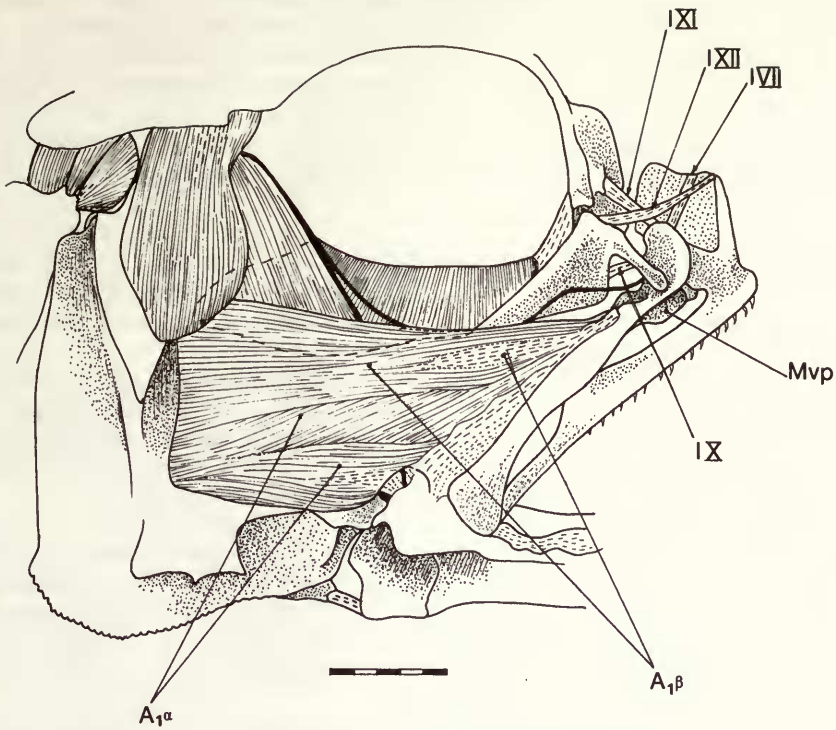


Fig. 3 *Ventrifossa occidentalis*; cranial muscles and ligaments in lateral view.

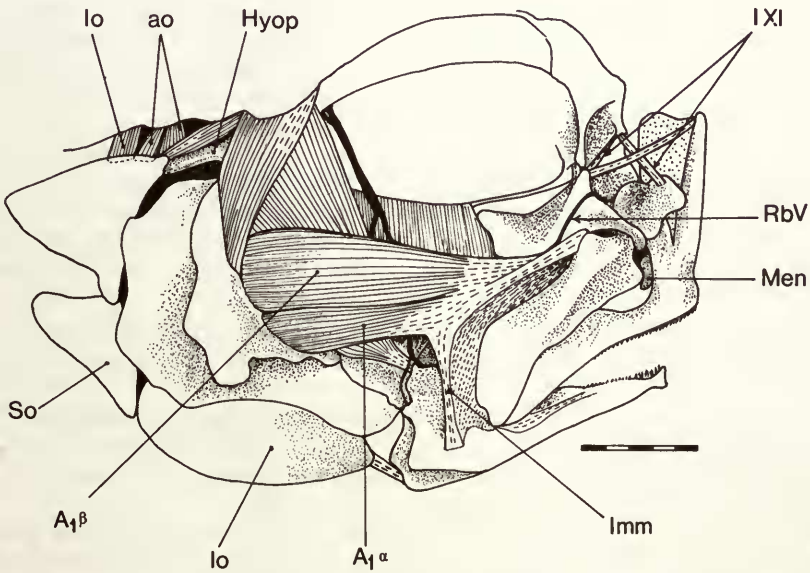


Fig. 4 *Cetonurus globiceps*; cranial muscles and ligaments in lateral view.

latter authors were concerned with describing the musculature in a functional context, although Casinos (1978) made some observations regarding the homology and evolution of certain adductor muscles. The taxonomic range of these authors' works is limited and the applicability of their functional conclusions to macrouroids in general requires a reappraisal in the light of morphological variations of which they were unaware.

NB. In the following descriptions the dorsal muscle of the adductor element (*levator maxillaris superioris* of authors) is referred to as A1 β ; its homology is discussed later, p. 34.

MACROURINAE

Type 1 morphology: two subgroups are recognised, (a) *Coryphaenoides*, *Abyssicola*, *Nezumia*, *Coelorinchus*, *Lionurus* (synonymised with *Coryphaenoides* by Iwamoto & Stein, 1973); *Nematonurus*, *Chalinura*; (b) *Macrourus*, *Trachonurus*.

The overall morphology of the adductor musculature is similar in the two subgroups, the only difference being the presence of an additional adductor element, A1 γ , in subgroup (a).

In all the taxa included in the Type I group the mouth is inferior or subinferior and the jaws relatively short; the premaxillary ascending process is at least 80% the length of the dentigerous ramus; the maxilla is a deep, stout bone with a markedly convex dorsal border.

The outer adductor muscle is thin but relatively deep and divisible into upper and lower parts which are either entirely separated (e.g. *Coryphaenoides*, Fig. 1), or partially so (e.g. *Coelorinchus*, Fig. 2). The lower part (A1 α) originates from the preopercular limb, and in *Coryphaenoides* from a prominent lateral flange of that bone (Fig. 1). The muscle inserts tendinously along the lower part of the maxillo-mandibular ligament. The upper part of the adductor (A1 β) originates from the preopercular limb and inserts *via* a stout tendon on to a ventromedial process of the maxilla; it is not joined to the maxillo-mandibular ligament.

Running dorsomedially to A1 β is a long spindle-shaped muscle here designated A1 γ (Fig. 3); see below. The fibrous part of the muscle originates from a long tendon which in turn stems from the fascia of A1 β . Insertion is *via* a cord-like tendon on the same medial process of the maxilla as A1 β . In *Lionurus*, there is a marked difference in the relative proportion of the fibrous part to the posterior tendinous part of the muscle between small and large-sized specimens. In a specimen of 150 mm TL, the muscle is 50% tendinous and 50% muscloses, whereas in a specimen of 225 mm TL, 75% of the muscle is fibrous. In *Abyssicola macrochir*, muscle A1 γ is a larger and deeper element than in any other taxon examined. Also, unlike other taxa of this group the muscle originates from a broad tendinous sheet stemming from the rim of the hyomandibula.

Muscle A2 is a deep, broad element whose medial fibres originate from the frontal, and those more lateral in position from the prootic and hyomandibula. A2 has a complex insertion in the lower jaw. Its posteromedial fibres insert into an aponeurosis which bifurcates into a vertical and a horizontal tendon. The vertical tendon inserts onto the coronomeckelian bone and continues to the dorsomedial surface of the narrow retroarticular, while the horizontal tendon runs forward into the mandibular cavity. The majority of fibres of A2 insert on the horizontal tendon, from which also originate those of the *mandibularis* section of the adductor A ω (Fig. 1). Muscle A ω lies mostly outside the mentomeckelian cavity, but with a small bundle of lateral fibres running forward into it.

The *levator arcus palatini* (Figs 1 & 2) is a long, pyramidal muscle running between the sphenotic and the lateral face of the hyomandibula; its outermost fibres insert on the edge of the preopercular limb.

The *dilatator operculi* (Figs 1 & 2) originates from the lateral hyomandibular fossa and inserts on the rim of the opercular facet. The *adductor* and *levator opercularis* muscles extend from the lateral border of the pterotic, the *adductor* inserting on the opercular process of the hyomandibula and the *levator* on the anteromedial face of the operculum (Figs 1 & 2).

The *adductor arcus palatini* occupies the floor of the orbit, its anterior fibres inserting on the broad concave surface of the palatine (Figs 1 & 2). Posteriorly, the muscle runs between the parasphenoid and the lateral faces of the entopterygoid and metapterygoid and the medial face of the hyomandibula.

Type II morphology. Macrourinae (part): *Ventrifossa*, *Cetonurus*, *Echinomacrus*, *Malacocephalus*, *Hymenocephalus*, *Odontomacrus*, *Sphagemacrus*, *Cynomacrus*, *Mataeocephalus*.

Taxa of this group have a terminal or subterminal mouth, with the exception of *Echinomacrus* in which it is inferior. The ratio of premaxillary ascending process to dentigerous ramus length varies from 30–33% in *Odontomacrus* and *Chalinura* to 50% in *Ventrifossa*. An opposite extreme is *Mataeocephalus* where the premaxillary ramus is 50% of the length of the ascending process (cf. Macrouroidinae, p. 15); in *Echinomacrus* and *Cetonurus*, the ramus and ascending process are of almost equal length.

The characteristic myological feature of this morphotype is that A1 is a single, or incompletely divided, deep element. *Ventrifossa occidentalis* is taken to illustrate the morphotype, representative of the majority of taxa (Fig. 3). *Echinomacrus* and *Cetonurus* which differ somewhat in detail from *Ventrifossa* are considered below.

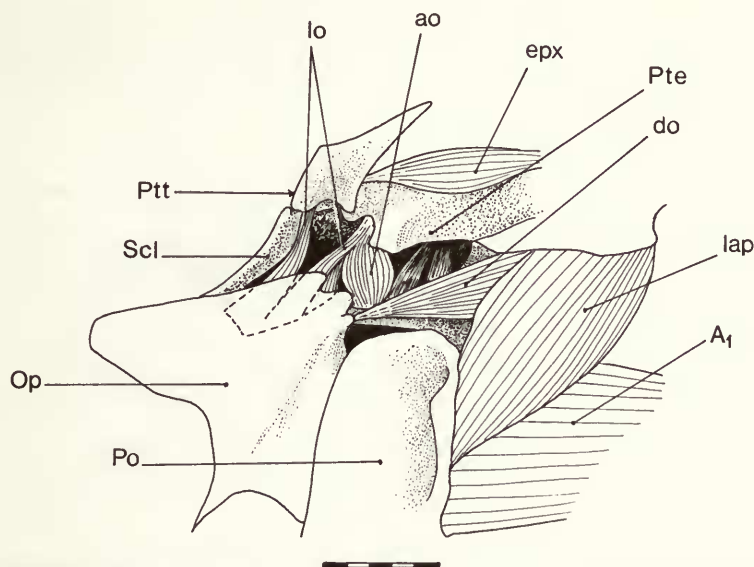


Fig. 5 *Cynomacrus piriei*; levator arcus palatini and opercular muscles in lateral view.

Muscle A1 originates posterodorsally from the upper part of the preopercular limb and ventrally from the preoperculum and quadrate (Fig. 3). The dorsal border of the muscle is almost horizontal, there being a slight concavity and tendinous area below the orbit. Dorsal fibres of the muscle insert on the inner aspect of the maxilla, while the remainder of the muscle, separated from the upper part by an internal aponeurosis, inserts into the anterior third of the maxillo-mandibular ligament. Along the centre of the muscle is an aponeurosis which is marked laterally by a change in muscle fibre direction—from almost horizontal (dorsally) to oblique (ventrally). The position of the aponeurosis is marked in taxa belonging to morphotype I by a complete or partial division of the muscle. In this respect *Cetonurus* resembles the latter taxa (Fig. 4).

Muscle A2 is a deep element originating from a cavity formed between the prootic and frontal, with fibres stemming from both bones. In *Cynomacrus* and *Odontomacrus* the anterior muscle fibres are vertically aligned or posteroventrally angled, in contrast to the more usual anteroventral angle present in *Ventrifossa* (Fig. 3). The insertion of muscle A2 in the lower jaw is via a cord-like tendon carrying outer fibres to the coronomeckelian bone and into a broad aponeurosis from which originates muscle A ω . The muscle is short, barely extending halfway along the mandible; only its dorsal fibres enter the mentomeckelian cavity.

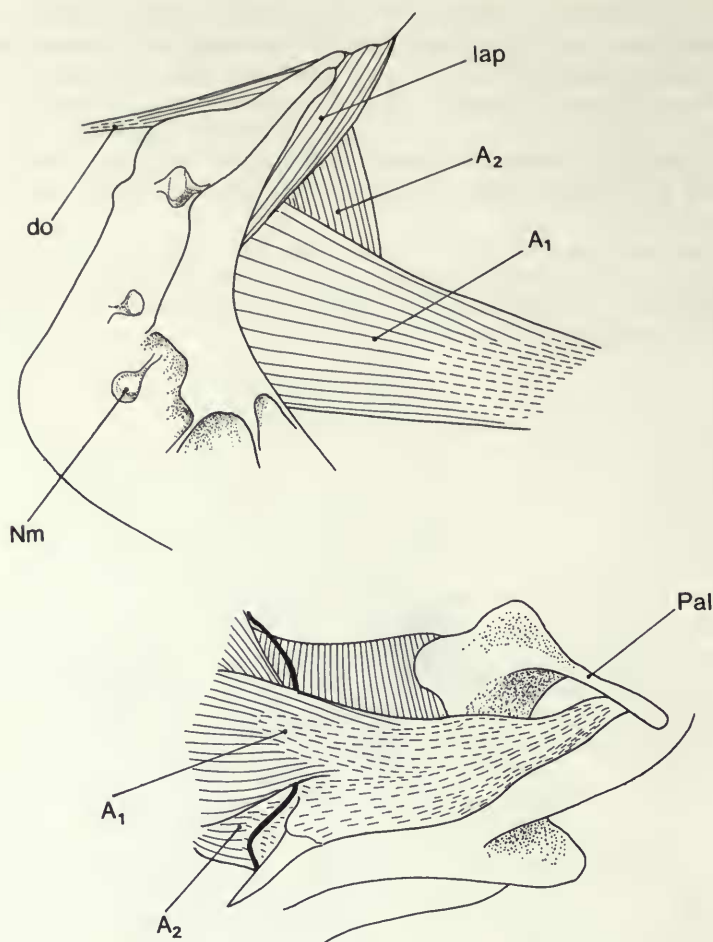


Fig. 6 Macrouroidinae; above, *Squalogadus modificatus*, preoperculum and associated muscles; below, *Macrouroides inflaticeps*, anterior of adductor musculature.

The *levator arcus palatini* is a large muscle in all Type II genera, extending from the sphenotic and pterotic to the lateral face of the hyomandibula, its anteroventral portion covering the postero-dorsal margin of A1. In *Cynomacrus* the *levator* is angled forward to a greater degree than in the other included taxa (Fig. 5).

The *dilatator*, *adductor* and *levator operculares* muscles are all well-developed. The *dilatator operculi* originates from a lateral hyomandibular fossa and the *adductor* from the ventral surface of the pterotic. Some fibres of the *adductor operculi* insert with those of the *dilatator* on the rim of the opercular condyle, but the majority insert on the opercular process of the hyomandibula. In *Cetonurus* the separate insertions of the muscle are further marked by the complete division of its body. The *levator operculi* is a long, deep muscle originating from the ventral surface of the pterotic and inserting along the anteromedial border of the operculum. In *Cynomacrus* the *adductor operculi* inserts entirely on the opercular process of the hyomandibula and the *levator operculi* is divided. The anterior segment of the *levator* shares a common origin with the *adductor operculi*, but the posterior segment originates from the posttemporal (Fig. 5); both segments insert together on the anteromedial face of the operculum. With respect to its posttemporal origin, the *levator* of *Cynomacrus* is similar to that of the gadoid *Lota* (see p. 32 and Howes, 1988).

The *adductor arcus palatini* extends the length of the parasphenoid and anteriorly inserts on the palatine; posteriorly it inserts on the ento- and metapterygoids and the medial face of the hyomandibula. In *Cetonus* the muscle extends only halfway along the length of the parasphenoid (Fig. 4).

MACROUROIDINAE

Two monotypic genera are included in this subfamily, *Macrouroides* and *Squalogadus*. Of the former, only a single, poorly preserved specimen of *Macrouroides inflaticeps* was available for examination. The specimen has a damaged and partially disarticulated skull and it has been impossible to ascertain precisely the configuration and insertions of the adductor muscles. Likewise, only a single specimen of *Squalogadus modificatus* is available for examination and only a partial dissection of the posterior region of the cheek musculature has been possible (Fig. 6).

Muscle A1 is a single element originating from the preopercular limb and inserting on to the upper part of the maxilla *via* the maxillo-mandibular ligament.

Muscle A2 is a thick, crescentic muscle stemming from the frontal and prootic; its insertions in the lower jaw and the extent of muscle A ω have not been ascertained in either taxon.

Table 1 Grouping of Macrourinae based on jaw and ventral gill-arch muscle morphotypes (see text, p. 58), compared with Okamura's (1970*b*) groupings

	Jaw muscles		Gill-arch muscles	Okamura's groups
Type 1a	<i>Abyssicola</i> <i>Coryphaenoides</i> <i>Nezumia</i> <i>Lionurus</i> <i>Nematonurus</i> <i>Chalinura</i>	(a)	<i>Abyssicola</i> <i>Coryphaenoides</i> <i>Coelorinchus</i> <i>Lionurus</i> <i>Nematonurus</i> <i>Chalinura</i> <i>Macrourus</i>	<i>Abyssicola</i> <i>Coelorinchus</i> <i>Macrourus</i>
Type 1b	<i>Macrourus</i> <i>Trachonurus</i>		<i>Trachonurus</i> <i>Malacocephalus</i> <i>Mataeocephalus</i> <i>Cetonus</i> <i>Echinomacrurus</i>	
Type II	<i>Ventrifossa</i> <i>Malacocephalus</i> <i>Hymenocephalus</i> <i>Odontomacrurus</i> <i>Cynomacrurus</i> <i>Mataeocephalus</i> <i>Macrosmia</i> <i>Cetonus</i> <i>Echinomacrurus</i> <i>Sphagemacrurus</i>	(b)	<i>Ventrifossa</i> <i>Hymenocephalus</i> <i>Nezumia</i> <i>Odontomacrurus</i> * <i>Cynomacrurus</i> *	<i>Ventrifossa</i> <i>Malacocephalus</i> <i>Odontomacrurus</i> <i>Cynomacrurus</i> <i>Cetonus</i> <i>Echinomacrurus</i> <i>Sphagemacrurus</i>

NB. * these two genera lack a palatine-lateral ethmoid ligament. According to Iwamoto & Stein (1973),

Lionurus, *Nematonurus* and *Chalinura* should be treated as subgenera of *Coryphaenoides*.

The following macrourine genera have not been examined, *Astenomacrurus*, *Cetonurichthys*, *Haplomacrurus*, *Lepidorynchus*, *Paracetonus*, *Parakumba*, *Pseudocetonus*, *Pseudonezumia*.

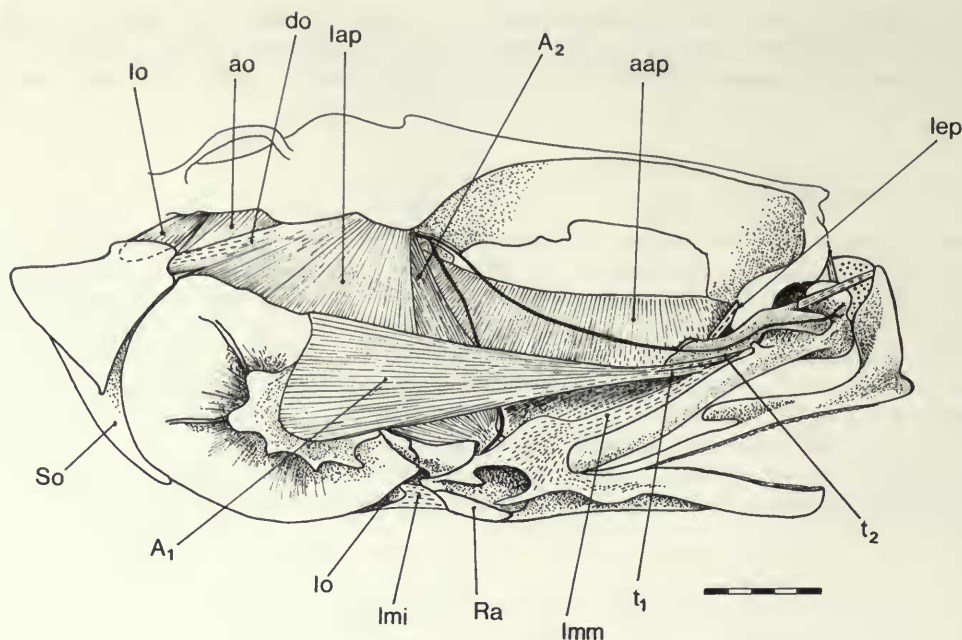


Fig. 7 Trachyrincidae: *Trachyrincus trachyrincus*; cranial muscles in lateral view.

The *levator arcus palatini* and *operculi* muscles are missing from the specimen of *Macrouroides*, but in the *Squalogadus* specimen there is a small *levator arcus palatini*, lying posterolaterally to the *adductor mandibulae* complex (Fig. 6).

The *adductor arcus palatini* is a thick element flooring the orbital cavity, inserting anteriorly on the palatine and posteriorly on the lateral surface of the ento- and metapterygoids.

Comparisons with gadoids

The presence of a dorsal section of the *adductor mandibulae* originating from the palatoquadrate was considered by Rosen & Patterson (1969: 361 *et seq.*) to be a specialisation of paracanthopterygian fishes. Fraser (1972) commented that a muscle of this type had developed in several acanthopterygian groups and could not be used as a character indicating phyletic relationships. He also pointed out that the number of taxa examined for this character by Rosen and Patterson was too few to make generalisations as to its occurrence and homology. Marshall & Cohen (1973) in referring to the so-called *levator maxillaris superioris* muscle note that '... character has received little comment; its distribution and taxonomic significance are at present in need of fuller survey'.

There has been much confusion concerning the identity of the dorsal adductor muscle in paracanthopterygians. Rosen (1962) and Rosen & Patterson (1969: 341 *et seq.*) referred to the element as a *levator maxillaris superioris* (i.e. the homologue of that muscle in the halecomorph *Amia*; see Allis, 1897). Previous authors, viz. Holmquist (1911) and Dietz (1921) had referred respectively to the muscle as A4 and A1 β . Later, Rosen (1973: 417) reformulated his ideas and, following Dietz, referred to the muscle as A1 β , a view supported by Winterbottom (1974a) and most subsequent authors. Casinos (1978: 443) continued to use the term *levator maxillaris superioris* '... because of functional reasons'.

Because the muscle in question lies lateral to the mandibular branch of the trigeminal (V) nerve, I concur with Winterbottom (1974a) in recognising it as part of muscle A1. Allis (1897: 581–2) comments that the '... course and position of the inferior maxillary nerve ... seems to lie always between A1 and A2 ...'; see similar remarks of Freihofer (1978: 17) and Howes (1985: 275).

In all gadiform fishes I have examined, apart from some macroroids noted above and the Trachyrincidae (see below), a dorsal division of muscle A1 is present. The various conditions of this, and other cranial muscles are as follows:

TRACHYRINCIDAE

(Figs 7 & 8)

The family (formerly recognised as a macroroid subfamily) contains two genera *Trachyrincus* and *Idiolophorynchus*. Species are characterised by their unique adductor muscle arrangement (described below), interopercular-preopercular-opercular ligamentous arrangement, nasal morphology, caudal skeleton (see Howes, 1988) and other features such as dorsal scutes (given in diagnosis for subfamily by Marshall, 1973). In trachyrincids the jaws are long, the length of the premaxillary ascending process being 50% of the ramus.

Muscle A1 is a single, narrowly triangular element which extends from the anterolateral face of the preoperculum to insert *via* a double tendon on the maxilla. The upper tendon (t2, Fig. 7) passes medially to insert close to the maxillary head while the lower (t1, Fig. 7) joins the maxillo-mandibular ligament to insert on the lateral face of a maxillary dorsal process. Casinos (1978: 443) is incorrect in stating that a maxillo-mandibular ligament is absent in *Trachyrincus*. A ventral tendon runs from the aponeurosis to the coronomeckelian bone; muscle A ω extends from the anterior part of the aponeurosis, the majority of fibres lying medial (outside) the mentomeckelian cavity.

The *levator arcus palatini* in contrast to that of macroroid taxa, is extended posteriorly and its anteroventral part is covered by the *adductor mandibulae*. The muscle originates dorsally from the sphenotic and pterotic, and medially from the hyomandibula; insertion is across the extensive dorsal face of the preoperculum.

The *dilatator operculi* originates from a common aponeurosis with the *levator arcus palatini* and has a strong tendinous insertion on the rim of the opercular condyle. The *adductor operculi* is a long muscle originating from the ventral surface of the pterotic and inserting for much of its length on the opercular process of the hyomandibula. Only the posterior fibres insert on the operculum, just medial to the insertion of the dilatator muscle. The *levator operculi* is a thin, narrow element running postero-laterally and inserting on the medial face of the small operculum.

The *adductor arcus palatini*, although extending the length of the parasphenoid is weakly developed anteriorly (of single fibre thickness) and does not insert on the palatine.

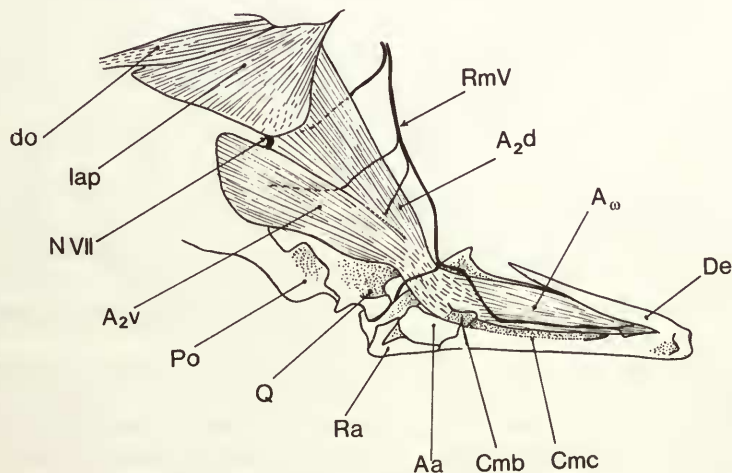


Fig. 8 *Trachyrincus trachyrincus*; medial view of inner adductor muscle and lower jaw.

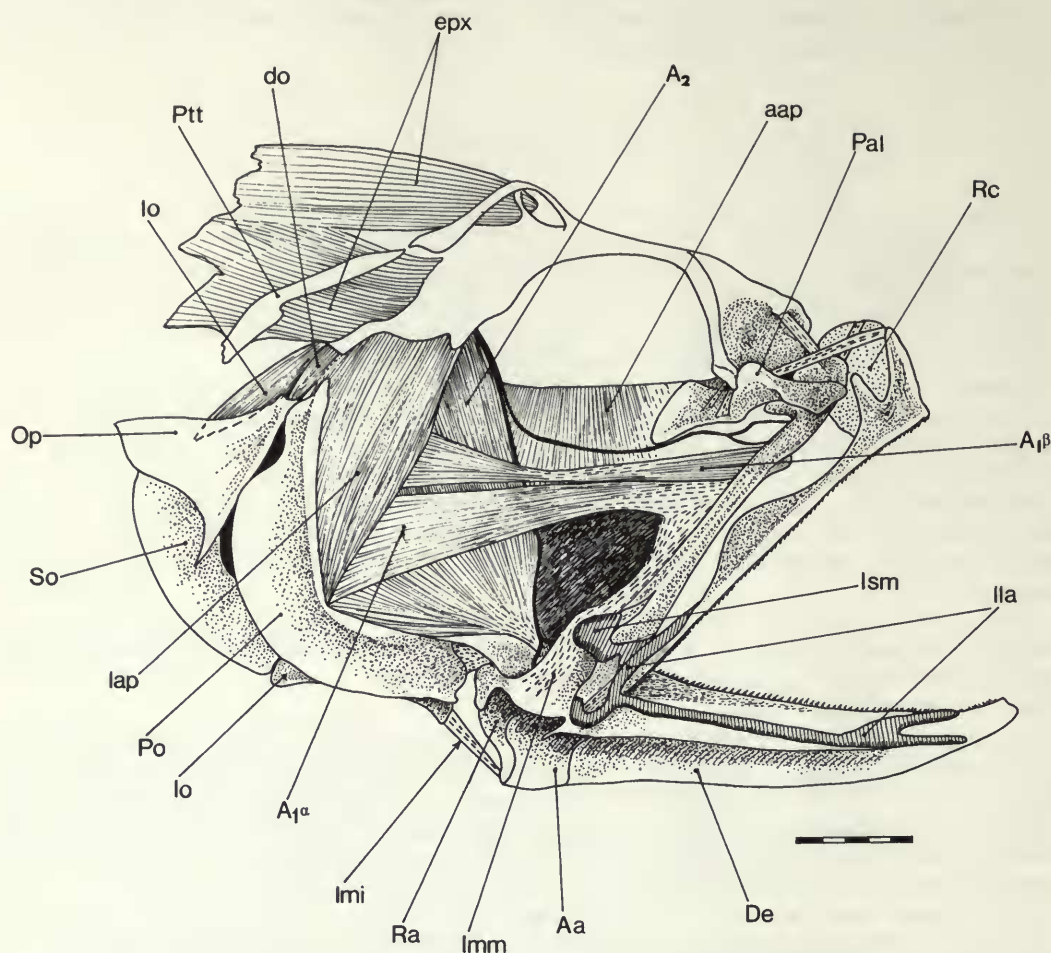


Fig. 9 Bathygadidae: *Bathygadus melanobranchus*; cranial muscles and ligaments in lateral view.

BATHYGADIDAE (Figs 9 & 10)

Formerly recognised as a subfamily of macrouroids, Howes (1988) referred the 'bathygadine' genera *Bathygadus* and *Gadomus* to the Gadoidei as a clade, here recognised as a family. A complete taxonomic diagnosis is in preparation but it can be stated here that the family is distinguished from other gadoid families by its lack of a caudal skeleton, derived RLA pectoral nerve pattern, reduced gill-filaments, reticulate scale pattern and myological synapomorphies detailed here.

Bathygadus and *Gadomus* have a terminal mouth with a wide gape, the jaws are long and slender. The outer adductor muscle is a thin, shallow sheet of fibres originating from the preoperculum and posterior margin of the hyomandibula. In most *Bathygadus* species it is clearly divided into ventral ($A1\alpha$) and dorsal ($A1\beta$) parts. However, in *B. favosus*, the two muscles can only be distinguished by their separate tendinous insertions on the maxilla. In the species where the $A1\alpha$ and $A1\beta$ parts remain separated, $A1\alpha$ joins a broad aponeurosis with the maxillo-mandibular ligament halfway

along the length of the maxilla. Muscle $A1\beta$ originates from the medial fascia of the *levator arcus palatini* muscle and is divided into anterior and posterior segments, the division being brought about by the muscle's tendinous constriction below the orbit. The anterior segment of $A1\beta$ inserts on the medial face of the maxillary process.

In *Gadomus* muscle $A1\alpha$ has a definite insertion on the outer aspect of the anterior part of the maxilla, and the maxillo-mandibular ligament is longer and narrower than in *Bathygadus*.

Muscle $A2$ is a large element originating from the hyomandibula, prootic and frontal and inserting on the lower jaw. Insertion is partly *via* a vertical tendon stretching down the medial face of the anguloarticular, and partly on a tendon inserting on the coronomeckelian bone and medial face of the anguloarticular. From these tendinous insertions stem the fibres of the mandibularis part of the adductor muscle ($A\omega$). The anterior half of $A\omega$ enters a long mentomeckelian cavity.

The *levator arcus palatini* is a large, deep element which inserts halfway down the preopercular limb and entirely covers the origin of muscle $A1$. The lateral posterodorsal fibres of the *levator* are inseparable from those of the *dilatator operculi*.

The *adductor arcus palatini* extends nearly the entire length of the parasphenoid, but anteriorly it is feebly developed, with widely spaced, tendinous bands of fibres; posteriorly the muscle inserts on the lateral face of the metapterygoid and the medial face of the hyomandibula.

As noted above, the anterior fibres of the *dilatator operculi* intermesh with the dorsoposterior fibres of the *levator arcus palatini*; those respective groups of fibres of both muscles originate from the hyomandibula, inserting together with the *adductor operculi* on the opercular condyle. The *levator operculi* is a well-developed element stemming from the pterotic and inserting along the posteromedial border of the operculum.

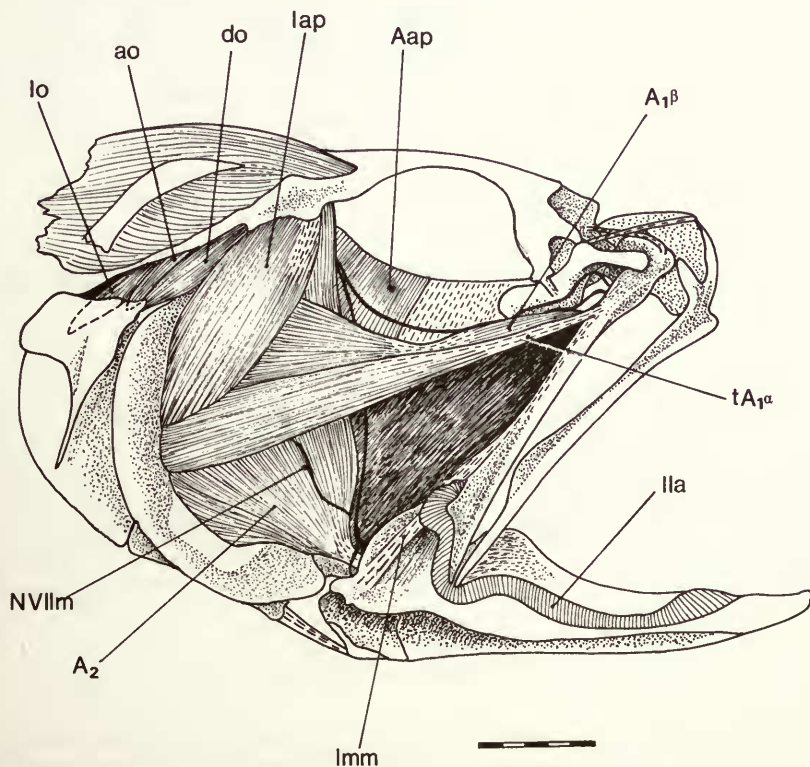


Fig. 10 Bathygadidae: *Gadomus longifilis*; cranial muscles and ligaments in lateral view.

MORIDAE

(Fig. 11)

In their overall morphology, the cranial muscles of morids are most similar to those of the Bathygadidae and *Gadomus* (Melanonidae). In *Halargyreus* (Fig. 11), *Pseudophycis* and *Antimora*, muscles A1 α and A1 β originate laterally to A2; A1 β is tendinously constricted below the orbit, its anterior expansion joining the insertion tendon of A1 α .

The *levator arcus palatini* is large, its ventral tip extending to a point halfway down the pre-opercular limb (cf. *Bathygadus*). The *adductor arcus palatini* is divided into posterior and anterior parts, the latter inserting on the entopterygoid and not the palatine as in most other gadoids.

In *Lepidion* (Fig. 10), muscles A1 α and A1 β are incompletely separated; both segments originate from a single body. The dorsal (A1 β) and ventral (A1 α) bundles insert on separate tendons beneath the orbit, which then join into a single muscle body lateral to the palatine before separating into their respective medial and lateral maxillary insertions.

The *levator arcus palatini* covers the upper part of A2, dorsally it joins the *dilatator operculi* along an aponeurosis. The *adductor arcus palatini* is feebly developed in its central portion; the anterior fibres insert on the palatine.

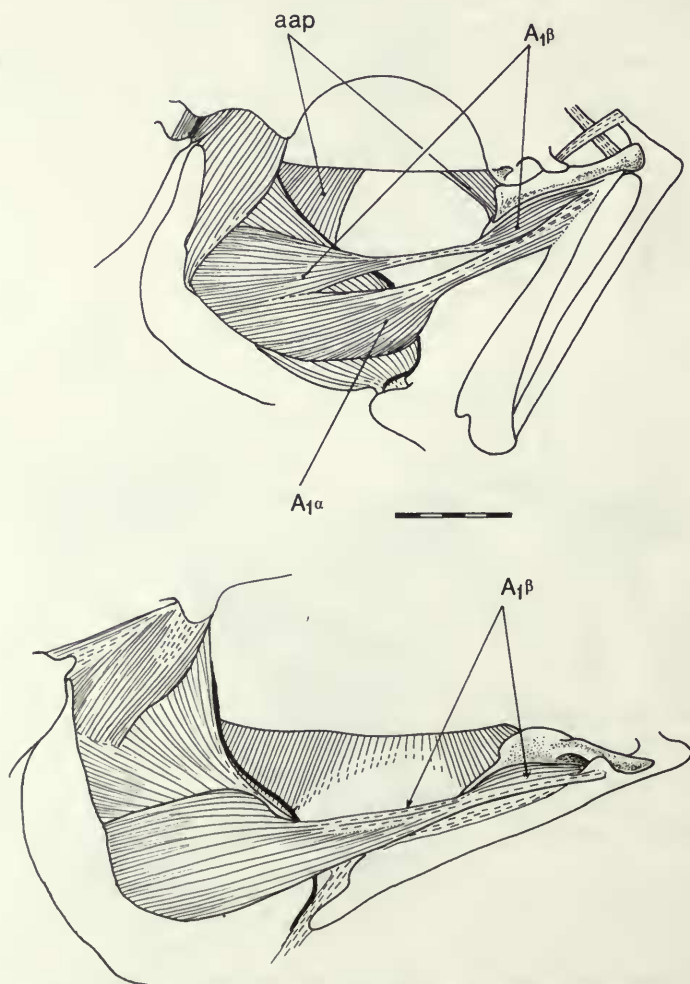


Fig. 11 Moridae: above, *Halargyreus affinis*; below, *Lepidion eques*; upper jaw and suspensorial muscles in lateral view.

MELANONIDAE

(Fig. 12)

In *Melanonus* muscles $A_{1\alpha}$ and $A_{1\beta}$ are inseparable at their origins which is from the fascia of muscle A_2 . The individual elements only become apparent above the jaw articulation. $A_{1\beta}$ is constricted into a tendon halfway along its length at the point where it is crossed transversely by a ligament running from the posterolateral edge of the palatine and the entopterygoid to the medial face of the second infraorbital. The anterior expansion of $A_{1\beta}$ inserts on the inner part of the maxillary head. The outer element, $A_{1\alpha}$, inserts *via* a separate tendon on to the outer face of the maxilla.

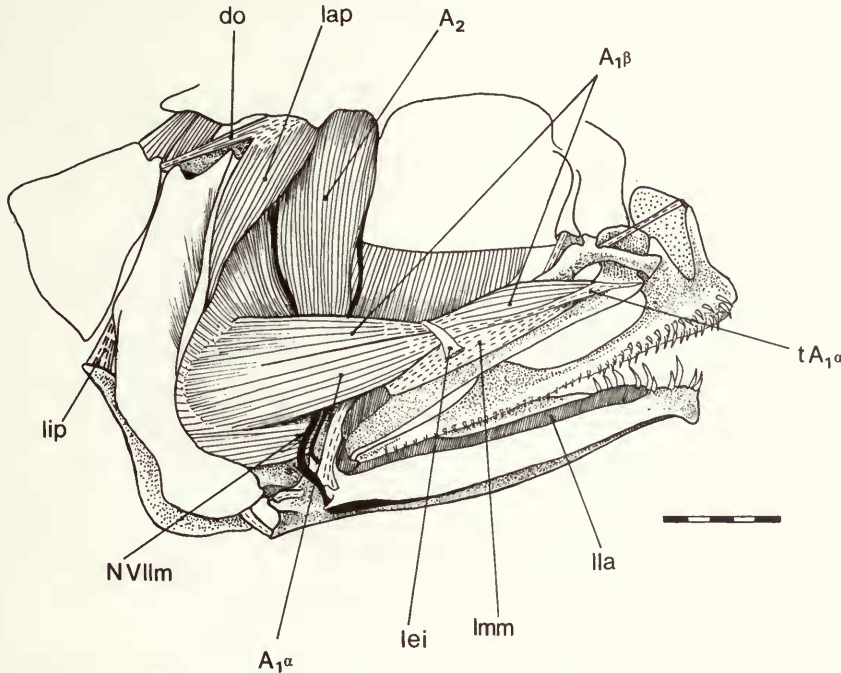


Fig. 12 Melanonidae: *Melanonus zugmayeri*; cranial muscles in lateral view (suboperculum removed).

Muscle A_2 is strongly developed, its anterior fibres being almost vertical. The muscle is partially divided by a hypertrophied *ramus mandibularis internus facialis* of the hyomandibularis VII nerve trunk (Fig. 12).

The *levator arcus palatini* shares an aponeurotic origin with the *dilatator operculi*. The *adductor arcus palatini* is well-developed, flooring the orbital cavity, and inserting anteriorly on the palatine.

The *adductor* and *levator operculares* muscles share a common origin from the ventral surface of the pterotic shelf. The *adductor* inserts both on the dorsomedial rim of the opercular condyle and the opercular process of the hyomandibula; the *levator* inserts along the dorsomedial border of the operculum:

STEINDACHNERIIDAE

(Fig. 13)

In *Steindachneria* muscle A_1 is large, originating from the lower half of the preopercular limb. Its fibres are angled anterodorsally, and dorsally the muscle is divided. The posterodorsal group of fibres insert on an aponeurosis from which stems a sausage-shaped segment of fibres running

forward to meet, laterally, the maxillo-mandibular ligament. From this point, the muscle becomes separated from the ligament and almost immediately inserts on the medial aspect of the maxillary head. This part of the muscle is identified as A1 β . The ventrolateral group of fibres inserts directly on the maxillo-mandibular ligament and is identified as A1 α .

Muscle A2 originates from the prootic, the sphenotic process and the upper part of the hyomandibula, its anterior fibres running almost vertically.

Insertion in the lower jaw is *via* a strong vertical tendon to the coronomeckelian bone and a broad aponeurosis from which originates A ω . No fibres of A2 insert on the anguloarticular. Muscle A ω is lanceolate, the majority of its fibres filling the mentomeckelian cavity.

The *levator arcus palatini* is moderately developed, originating from the sphenotic process and pterotic, and inserting in a lateral cavity of the hyomandibula. The muscle lies lateral to A2, but its

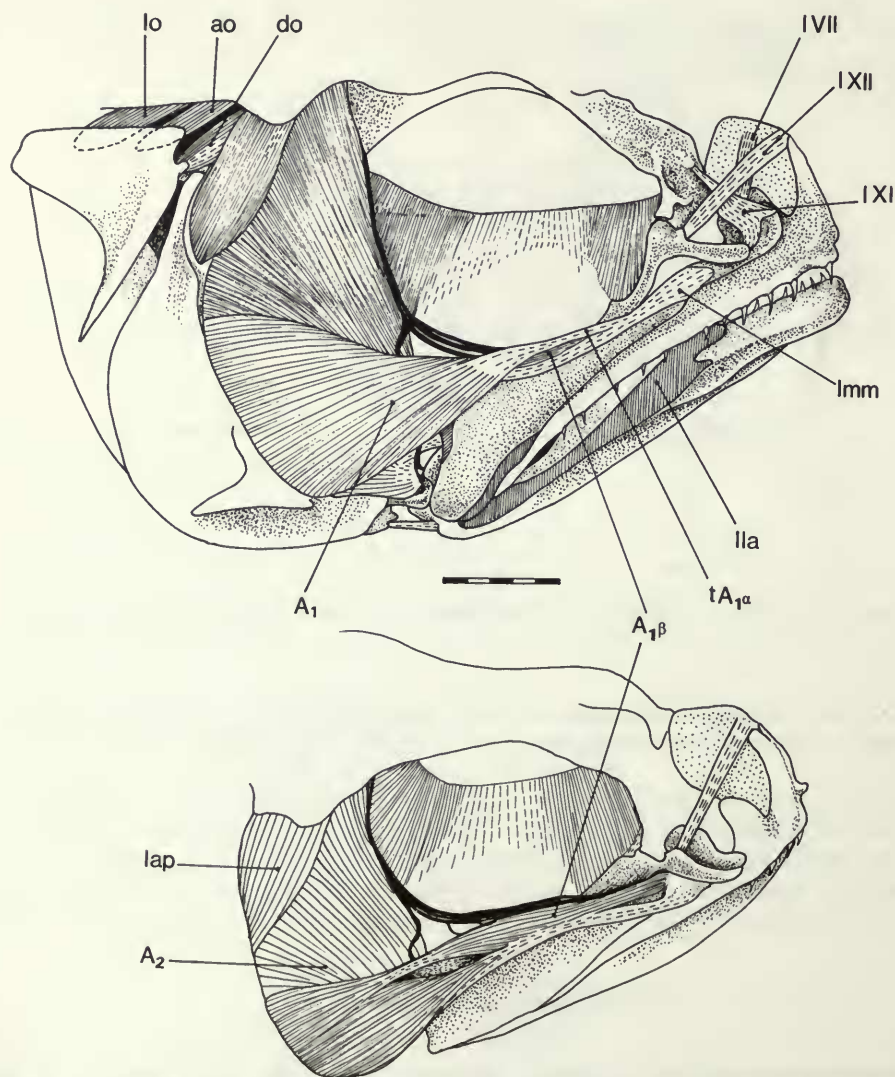


Fig. 13 Steindachneriidae: *Steindachneria argentea*: cranial muscles in lateral (above) and dorsolateral (below) views. NB. Not all the upper jaw ligaments are shown in the lower drawing.

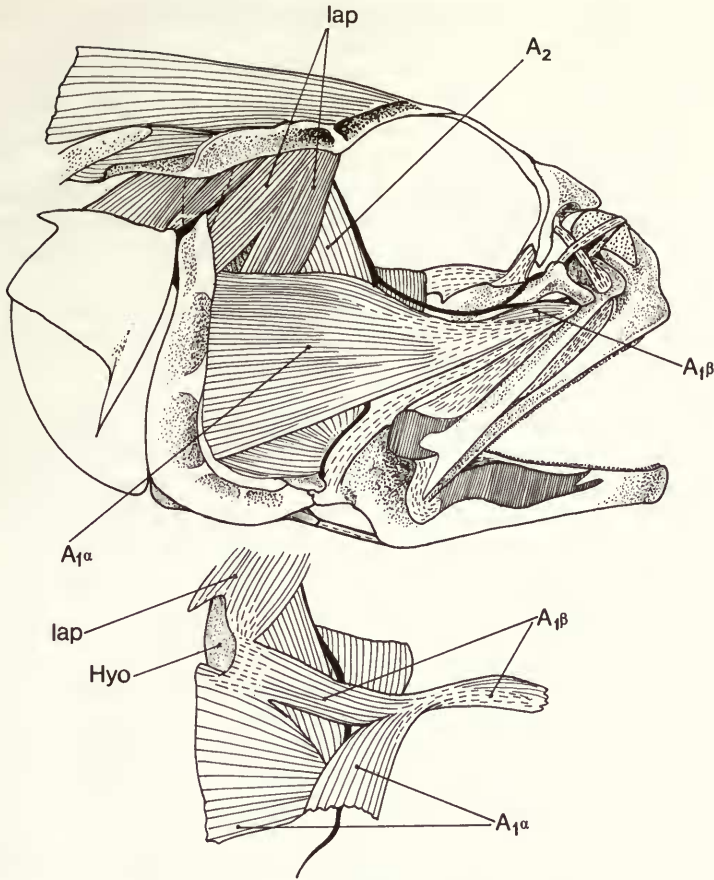


Fig. 14 Euclichthyidae: *Euclichthys polynemus*; above, cranial muscles in lateral view; below, posterior associations of muscle $A_1\beta$; $A_1\alpha$ reflected.

ventral tip does not reach as far as the origin of muscle A_1 . The *adductor arcus palatini* is well-developed posteriorly and anteriorly, where it inserts on the palatine but its central portion is reduced to a few widely spaced fibres which are well-separated from the dorsal margin of the pterygoid series.

Rosen & Patterson (1969, fig. 44a) depict the adductor musculature of *Steindachneria*. However, my observations are not completely in accord with theirs, since they show muscles $A_1\alpha$ and $A_1\beta$ separated for their entire lengths, and a fully developed *adductor arcus palatini*.

The *dilatator*, *adductor* and *levator operculares* muscles are as described for *Melanonus*.

EUCLICHTHYDIDAE

(Figs 14 & 15)

The *adductor mandibulae* muscle is a thick, deep element originating from the upright limb of the preoperculum; it comprises superficial, $A_1\alpha$, and medial, $A_1\beta$, elements which have complex associations posteriorly.

Muscle $A_1\beta$ is, posteriorly, a shallow, band-like muscle, having its origins aponeurotically from, dorsally, the *levator arcus palatini*, and ventrally, the dorsomedial surface of $A_1\alpha$, thus partially dividing the latter. Anteriorly, muscle $A_1\beta$ becomes bulbous and transversely expanded, joining with $A_1\alpha$ before separating from it to insert on the ventromedial surface of the maxillary head.

Muscle A1 α is tendinous anteriorly and joins the maxillo-mandibular ligament together with A1 β ; its insertion is on the dorsolateral surface of the maxilla.

Muscle A2 is well-developed, originating from the sphenotic and the dorsolateral surface of the hyomandibula. In the lower jaw, A2 joins a band-like aponeurosis, from which originates A ω ; a strong vertical tendon runs from the aponeurosis to the coronomeckelian bone. Muscle A ω is long and shallow, lying within the mentomeckelian cavity for most of its length.

The *levator arcus palatini* originates from the sphenotic and pterotic; it bifurcates ventrally, the anterior branch inserting on the hyomandibula and having an aponeurotic connection with muscle A1 β (see above and Fig. 14); the posterior branch inserts on the preoperculum and overlaps the posterodorsal edge of A1 α .

The *adductor arcus palatini* is confined to the posterior part of the parasphenoid; it inserts on the lateral faces of the ento- and metapterygoids. A unique feature of this muscle is that it is divided by a strong ligament running from the lateral ethmoid and palatine to the medial face of the hyomandibula (see p. 7 and Fig. 15).

The *dilatator operculi* is a spindle-shaped muscle extending from the pterotic to the opercular process. The *adductor operculi* runs almost laterally from the underside of a pterotic shelf to insert entirely on the opercular process of the hyomandibula; the *levator operculi* is an extensive muscle whose insertion extends along the entire dorsal border of the operculum.

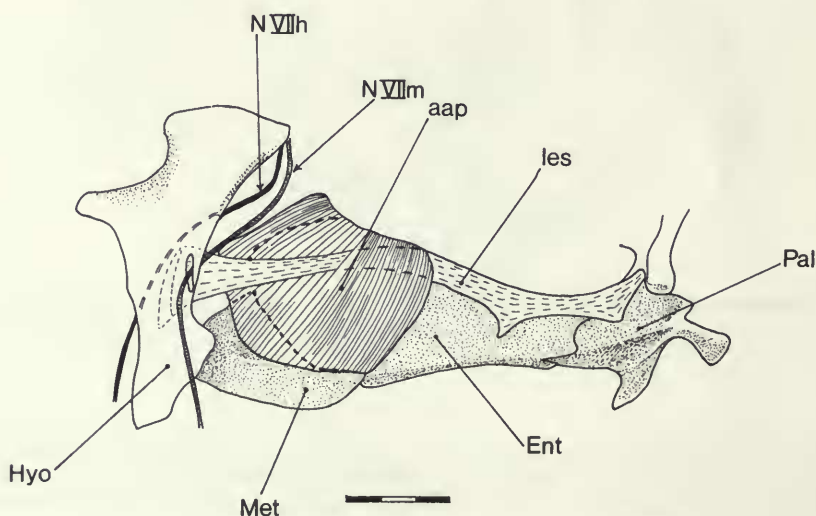


Fig. 15 Euclichthyidae: *Euclichthys polynemus*; *adductor arcus palatini* muscle and associated elements.

MERLUCCIIDAE

(Figs 16–18)

The following descriptions are based on three genera, *Merluccius*, *Macruronus* and *Lyconus*; *Lyconodes* has not been examined.

In *Merluccius* (Fig. 16) muscle A1 α is a thin, shallow element, stretching from a tendinous origin on the preoperculum across the face of muscle A2 to insert *via* a cord-like tendon halfway along the maxilla where it joins the maxillo-mandibular ligament. Muscle A1 β is a deep element having its origin from the meta- and entopterygoid and the palatine. It passes *medial* to the ramus mandibularis of the trigeminal nerve. The part of the muscle originating from the palatine is thick and bolster-like (Fig. 16). Insertion of A1 β is across a wide area of the medial face of the maxilla.

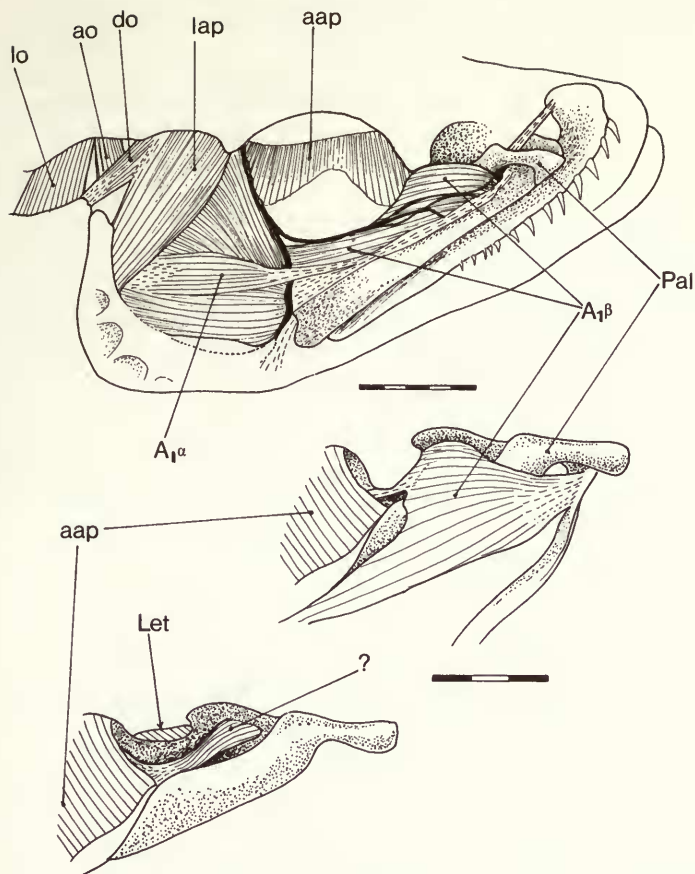


Fig. 16 Merlucciidae: *Merluccius merluccius*; cranial muscles in lateral view; above, entire; centre, palatine portion of muscle $A_1\beta$ (superficial); below, after removal of superficial muscle.

The *levator arcus palatini* is well-developed and lies lateral to the *adductor mandibulae* A2, but does not cover the origin of A1. The *adductor arcus palatini* floors the orbital cavity and inserts on the palatine. An unusual feature is the presence of a separate, small muscle running from the medial face of the palatine to the lateral face of the ethmoid bloc (Fig. 16). The muscle stems from the fascia of the *adductor arcus palatini*; in some specimens there are no muscle fibres, but only a narrow sheet of connective tissue.

The opercular muscles are well-differentiated, although the *dilatator operculi* shares an aponeurotic origin with the *levator arcus palatini*.

In *Macruronus* (Fig. 17), muscle $A_1\alpha$ is a thick, bulky element almost covering the lateral face of A2. In the pinnate arrangement of its fibres, the muscle differs from that in the taxa so far considered. Insertion is on the dorsal maxillary process via a thick tendon. Muscle $A_1\beta$ originates from the outer rim of the quadrate, the entopterygoid and a lateral cavity of the palatine; insertion is on the medial face of the maxillary head. The position of the ramus mandibularis of the trigeminal nerve lies posterior to the origin of $A_1\beta$.

Muscle A2 originates from the dorsomedial face and anterior rim of the hyomandibula and from the prootic. Insertion is via a lateral tendon to the coronomeckelian bone and a medial aponeurosis from which stems A_0 ; the latter lies entirely within the mentomeckelian cavity.

The *levator arcus palatini* is small, its ventral portion covered by $A_1\alpha$; insertion is into a small lateral hyomandibular cavity. The *adductor arcus palatini* is divided into anterior and posterior

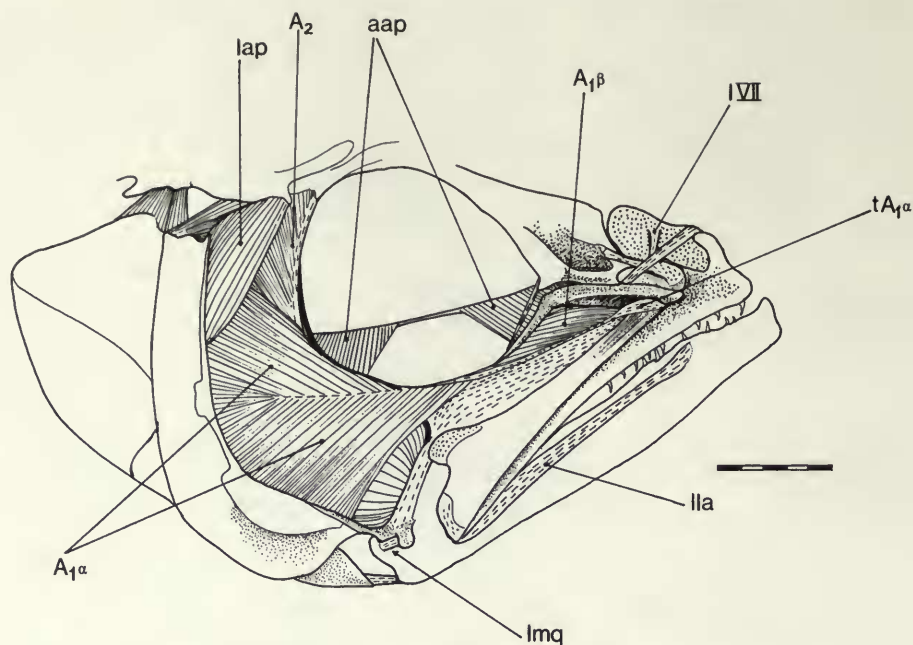


Fig. 17 Merlucciidae: *Macruronus magellanicus*; cranial muscles in lateral view.

portions, the former inserting into the medial cavity of the palatine. The *adductor operculi* inserts entirely on the opercular process of the hyomandibula.

In *Lyconus* (Fig. 18), muscle A1α is a narrowly triangular element whose area of origin extends from the central to the upper part of the preopercular limb. Fibre direction in the anteroventral section of the muscle is at almost 45° to that of the dorsal part. Insertion is *via* a long tendon on to the dorsal aspect of the maxilla. Muscle A1β resembles that of *Merluccius* in that it originates *medially* to the ramus mandibularis of the trigeminal nerve. The muscle's origins and insertions are complex; a posterior segment originates from the metapterygoid, a narrow, medial segment from the rim of the entopterygoid, and a long anterior segment from the concave lateral face of the palatine. The posterior segment runs into a long tendon, separate from that of the single tendon shared by the medial and anterior segments. The two tendons run forward to share a common insertion on the dorso-medial part of the maxillary head.

Muscle A2 is large, originating from the sphenotic and pterotic, its anterior fibres running almost vertically into the lower jaw.

The *levator arcus palatini* is a small unipinnate muscle originating from the sphenotic and pterotic; its insertion on the preopercular limb is above the origin of A1α. The *adductor arcus palatini* is well-developed, flooring the orbital cavity and, anteriorly, inserting on the palatine.

As only the type specimen of *Lyconus brachycolus* was available it has not been possible to make a sufficiently extensive dissection to ascertain the morphology of the other cranial muscles.

GADIDAE

(Fig. 18)

The following descriptions are based on three genera, *Gadus* and *Merlangius* (Fig. 18). These taxa differ from all those previously described in that muscle A1α is merely a thin, flat sheet of fibres stemming from the lateral body of A2 (as reported for *Microgadus* by Rosen, 1962). The separation of A1α from A2 is marked by the course of the ramus mandibularis of the trigeminal nerve, which

passes medial to the segment; the separated fibres insert on the dorsal aspect of the maxilla *via* the maxillo-mandibular ligament.

Muscle $A_1\beta$ is a noticeably stout muscle and also differs from the previously described conditions in that it originates tendinously from the lateral face of the hyomandibula, passing forward between muscles A_2 and A_3 and lateral to the ramus mandibularis nerve (*cf.* medial in *Merluccius*). The muscle is deep and parallel fibred, running against, but not attaching to, the palatine; insertion is on the ventral medial edge of the maxillary head.

Holmquist (1911: 12–17) has adequately described and illustrated the origins and insertions of the deeper adductor and the suspensorial and opercular muscles in *Gadus*; I find little variation from this condition in other gadid genera examined. It should be noted here, however, that the *levator arcus palatini* inserts on a lateral shelf or slope of the hyomandibula. Although in *Gadus*, the *levator* is, for the most part, covered laterally by muscle A_2 , in *Merlangius*, A_2 originates from below the hyomandibular shelf, thus leaving the *levator* exposed laterally and its outermost fibres lying in the same lateral plane as those of A_2 . The adductor muscles A_2 and A_3 are further discussed below (p. 41).

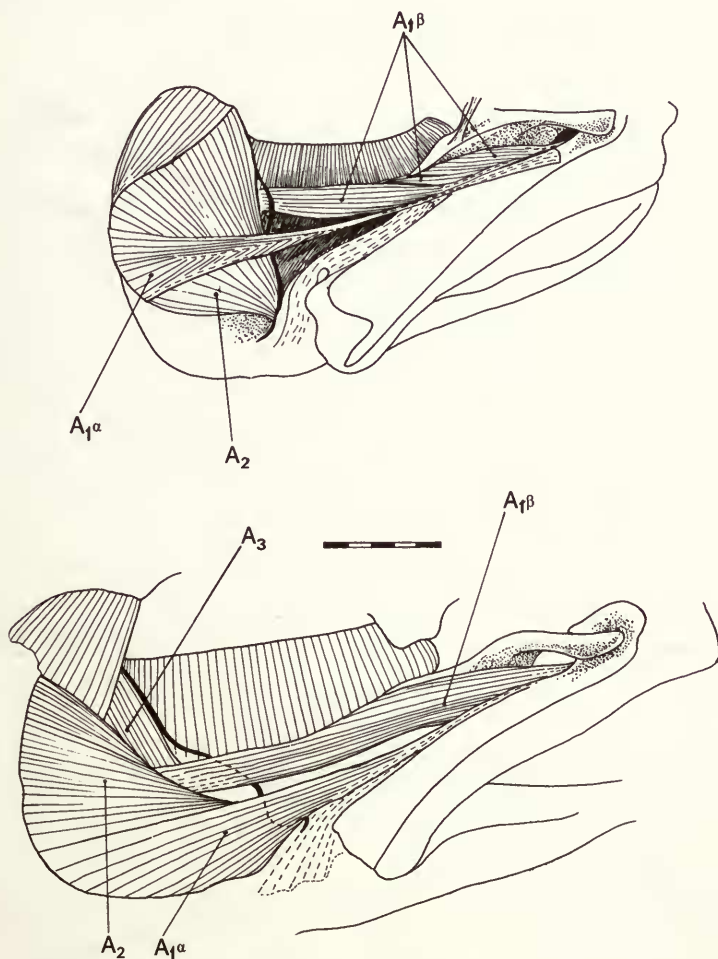


Fig. 18 Merlucciidae: above, *Lyconus brachycolus*, jaw and suspensorial muscles in dorsolateral view. Gadidae; below, *Merlangius merlangus*, jaw and suspensorial muscles in lateral view.

RANICEPITIDAE

(Fig. 20)

Howes (1987) recognised *Raniceps* as belonging to a distinct family on the basis of its sharing with certain phycids and the Muraenolepididae a tendinous attachment of the *rectus communis* muscle and the derived arrangement of the adductor musculature now described.

Muscle $A1\alpha$ is a small, spindle-shaped element, originating from the anterolateral face of $A2$. It runs alongside $A1\beta$, to which it is closely applied, and inserts *via* a long tendon on the dorsolateral face of the maxilla.

Muscle $A1\beta$ is a broad, band-like element having its origin tendinously from the hyomandibula and passing between muscles $A2$ and $A3$; anteriorly, the muscle becomes bulbous and inserts on the ventral surface of the maxillary head.

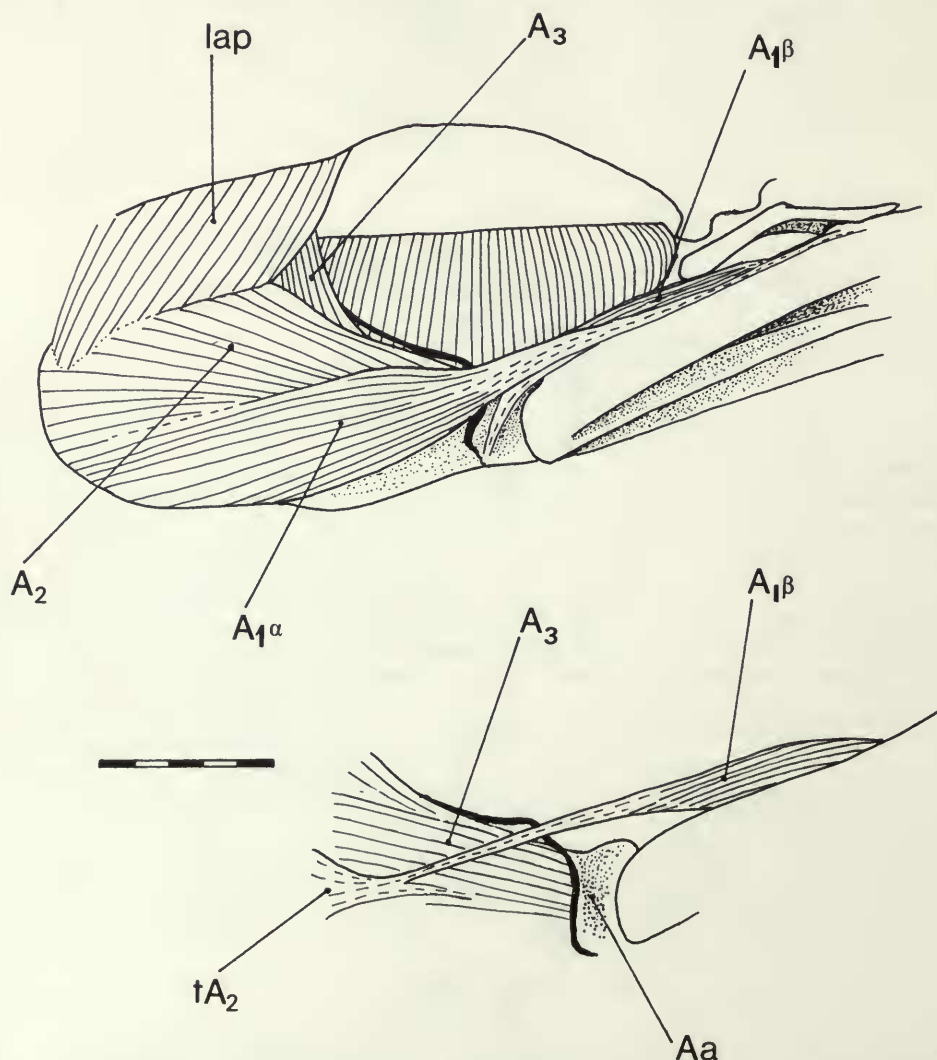


Fig. 19 Gadidae: *Molva molva*; jaw and suspensorial muscles in lateral view; above, entire; below, with outer adductor element removed to expose origin of $A1\beta$. Mandibularis branch of trigeminal nerve in solid black.

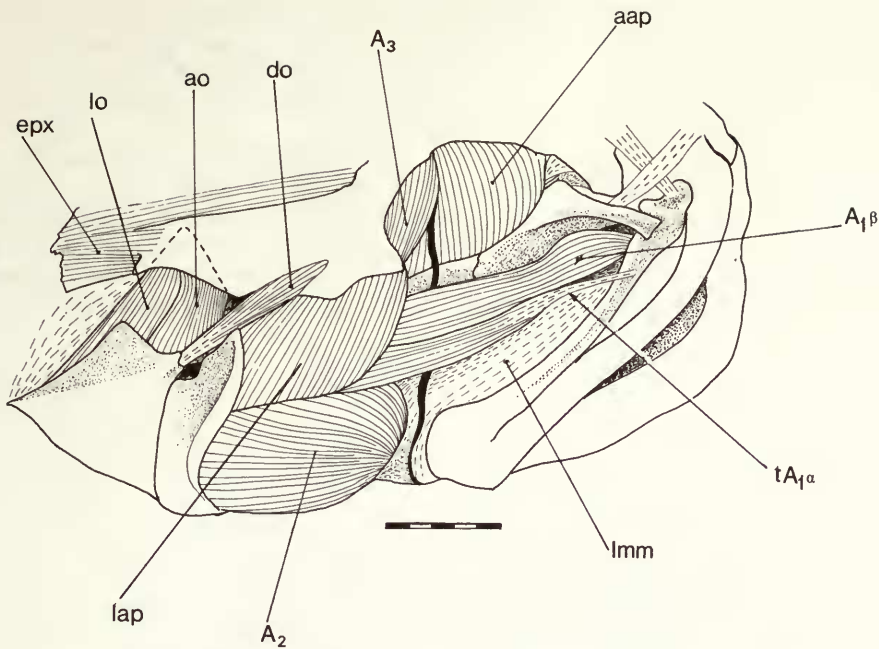


Fig. 20 Ranicipitidae: *Raniceps raninus*; cranial muscles in dorsolateral view.

Muscles A2 and A3 are thick, bulbous elements, the former originating from the preoperculum and hyomandibula, and the latter from the pterosphenoid and prootic. Both muscles join a common aponeurosis in the lower jaw from which A ω originates.

The *levator arcus palatini* is also a thick, bulbous element, stemming from the sphenotic and pterotic to insert on the hyomandibula and preoperculum. The lateral fibres of the *levator* meet those of adductor A2 along a near vertical raphe. The *adductor arcus palatini* is well-developed and floors the orbital cavity. The anterior fibres do not, however, insert on the palatine but remain within the confines of the entopterygoid.

The *dilatator operculi* is a narrow, ribbon-like muscle sharing a common origin with the posterior fibres of the *levator arcus palatini*; it inserts tendiously on the rim of the opercular facet. The *adductor* and *levator operculares* muscles share a common origin from beneath the pterotic and are separable only because of their insertions. The *adductor* inserts entirely on the opercular process of the hyomandibula; the *levator* along the dorso-medial surface of the operculum.

PHYCIDAE

(Fig. 21)

Urophycis is taken as the taxon representing this family but in at least one myological character both it and *Phycis* differ from other genera regarded as belonging to the family (see below).

In *Urophycis* (Fig. 21), fibres of muscle A1 share a common origin from the preopercular margin with those of A2. A1 separates from the body of A2 above the jaw articulation, its fibre direction varying from horizontal to 45°, and inserts *via* a long tendon on the anterodorsal process of the maxilla. Ventromedially, the insertion of A1 α joins the maxillo-mandibular ligament.

Muscle A1 β is a thick, cylindrical element originating, medially to A2, from the anterior rim of the hyomandibula. The muscle passes laterally to the ramus mandibularis of the trigeminal nerve, becoming slightly indented on its medial face below the orbit, and inserting muscously on to the ventral surface of the maxillary head.

Muscles A2 and A3 join a common aponeurosis medial to the anguloarticular (only a few fibres insert on the dorsal rim of the bone); the aponeurosis divides into medial and lateral tendons, the lateral one inserting on the coronomeckelian bone, while the medial branch forms the site of origin for muscle A ω . This muscle fills the mentomeckelian cavity with only a thin layer of fibres passing outside the cavity along the medial face of the dentary.

The *levator arcus palatini* is extensive and lies between A2 and A3; its dorsoposterior part can only be distinguished as a *dilatator operculi* by the insertion of those fibres on the rim of the opercular facet. The *adductor operculi* runs from the pterotic to the opercular process of the hyomandibula; the *levator operculi* inserts on the medial rim of the operculum. *Urophycis* is unusual in that a segment of epaxial muscle runs anteroventrally from the supracleithrum to insert on the medial face of the operculum. The posteroventral border of the muscle meets a part of the

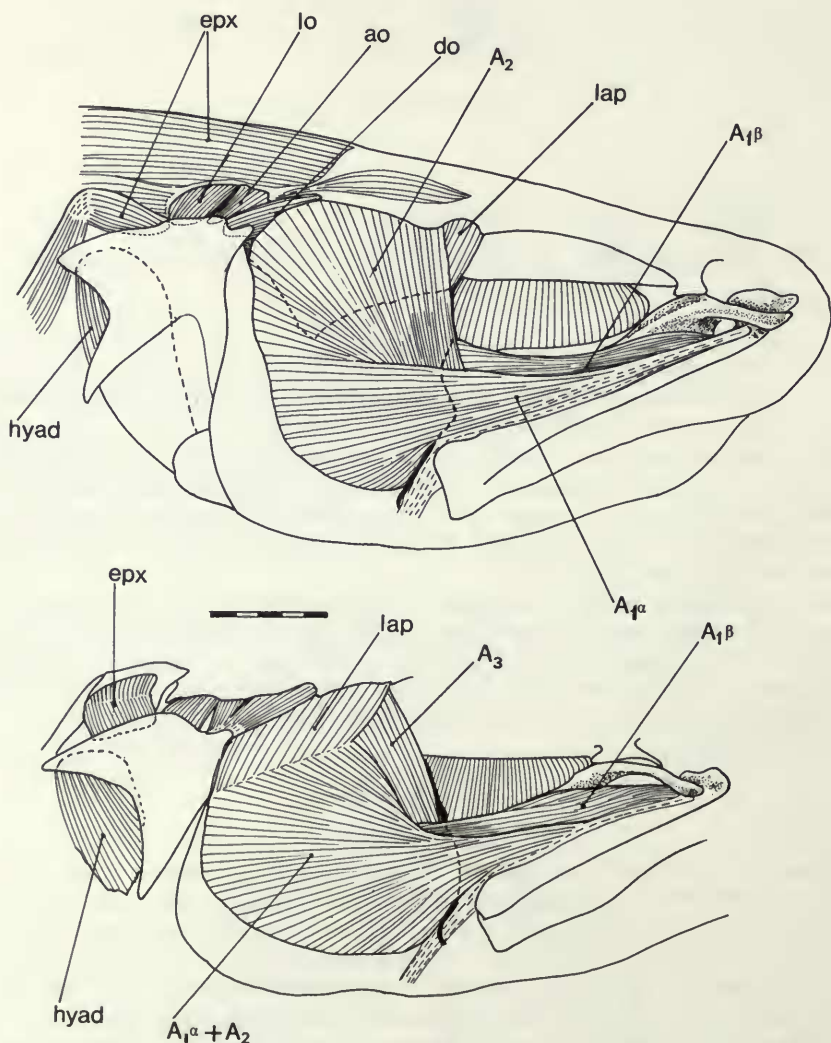


Fig. 21 Phycidae: above *Urophycis regia*; cranial muscles in lateral view. Lotidae: below, *Lota lota*; cranial muscles in lateral view; extent of *levator arcus palatini* and pathway of ramus mandibularis are indicated by dashed lines.

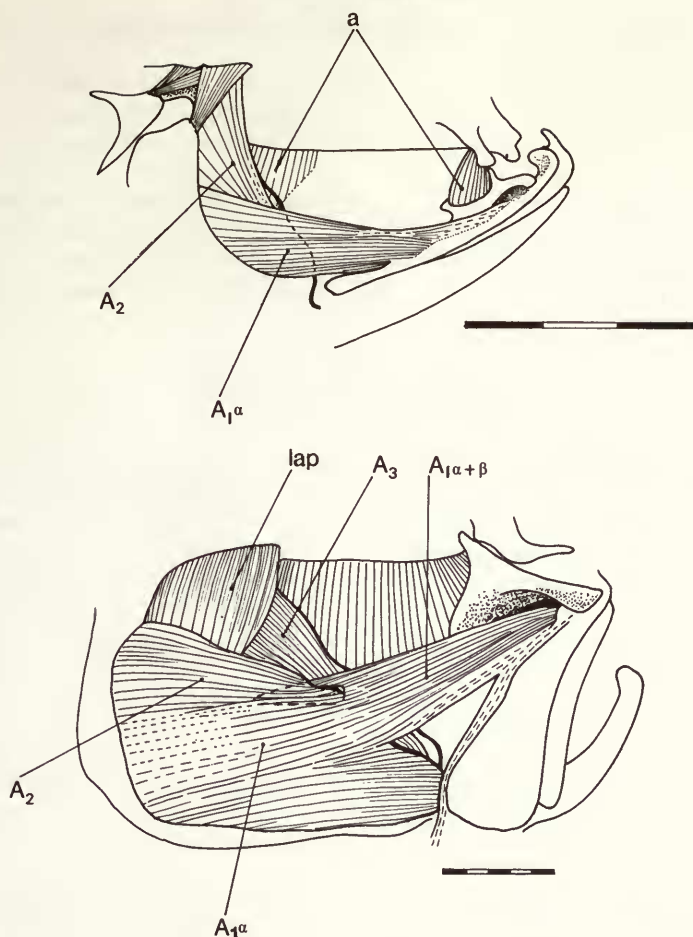


Fig. 22 Bregmacerotidae (above): *Bregmaceros atlanticus*. Muraenolepididae (below): *Muraenolepis microps*. Cranial muscle in lateral view (posterior extent of $A_1\beta$ indicated by dashed lines).

hyohyoidei adductores which extends from the last branchiostegal ray almost to the dorsal margin of the operculum. The *epaxialis* segment is less well-developed in *Phycis* and such an arrangement is absent in other phycids (see Howes, 1988).

LOTIDAE

(Figs 19; 21)

In *Lota* (Fig. 21) muscle $A_1\alpha$ is only differentiable from A_2 anteriorly by the separation of a bundle of lateral fibres which insert, *via* a long tendon, on the dorsal process of the maxillary bone. Muscle $A_1\beta$ originates from the anterior rim of the hyomandibula, medial to A_2 . A ventral tendon of $A_1\beta$ meets $A_1\alpha$ at the anterior border of A_2 ; the fibres of muscles $A_1\alpha$ and $A_1\beta$ are indistinguishable for a short distance prior to separation. $A_1\beta$ inserts on the ventromedial face of the maxillary head. The ramus mandibularis of the trigeminal nerve passes medial to $A_1\beta$, crosses above the lower jaw insertion of A_2+3 , and then passes medial to $A_1\alpha$.

Muscle A_3 is separated dorsally from A_2 by $A_1\beta$, the two former elements joining in a common aponeurosis from which A_{ω} originates.

The *levator arcus palatini* is not covered by A_2 as in the *Phycidae*, its lateral fibres lying in the

same plane and meeting aponeurotically those of A2. The ventral surface of the levator is bevelled to accommodate the medial surface of A2.

The opercular muscles are similar to those described for *Urophycis* and, as in that taxon, a segment of epaxial muscle inserts on the medial border of the operculum. Its site of origin, however, is the posttemporal rather than the supracleithrum as in *Urophycis* (but cf. *Muraenolepis*, below).

In *Molva* (Fig. 19), muscle A1 β occupies a position similar to that in *Gadus* and *Merlangius* but comprises a long tendon stemming from the point of origin on the hyomandibula and expanding anteriorly into a thick bundle of fibres which inserts on the maxillary head.

Muscle A2 runs from the lateral face of the hyomandibula and preoperculum to insert with A3 on an aponeurosis from which muscle A ω also originates.

MURAENOLEPIDIDAE

(Fig. 22)

In *Muraenolepis* (Fig. 22) muscle A1 has its origins lateral and medial to A2. Its lateral origin is from a thin tendinous sheet covering the face of A2; its medial origin is from a tendinous fascia on the inner aspect of that muscle. The two bodies of the muscle join into a single element anterior to the border of A2. The lateral part of A1 (A1 α) inserts tendinously on the dorsal aspect of the maxilla; the ventral border of the insertion tendon joining the maxillo-mandibular ligament. The main portion of A1 (A1 β) inserts on the ventromedial aspects of the maxillary head.

Muscle A2 is large, covering most of the *levator arcus palatini* laterally. It converges with muscle A3 into a thick tendon medial to the anguloarticular. A stout subbranch of the tendon inserts on the coronomeckelian bone. Muscle A ω extends from the principal part of the tendon; only its anterior tip enters the small mentomeckelian cavity. Muscle A3 is divided from A2 by the *levator arcus palatini* which is a large, laterally bulbous muscle, originating from the sphenotic and inserting into a shallow cavity on the lateral face of the hyomandibula. The *adductor arcus palatini* is well-developed, flooring the orbital cavity and inserting anteriorly on the palatine.

The opercular muscles are well-differentiated from one-another; the *dilatator* is a narrow, spindle-shaped element inserting on the long anterior process of the operculum; the *adductor* and *levator operculares* originate from the underside of the pterotic and insert close together on the anteromedial face of the operculum (see Howes, 1988, fig. 5). As in *Urophycis* and *Lota*, a segment of epaxial musculature inserts on the medial face of the operculum, being narrowly separated from the *hyohyoidei adductores*. As in *Lota*, the site of origin of the epaxial segment is the posttemporal (see Howes, 1988, fig. 5).

BREGMACEROTIDAE

(Fig. 22)

In *Bregmaceros* (Fig. 22) muscle A1 is thin and shallow and incompletely divided. However, below the eye there is a strong, dorsal tendon and medial aponeurosis with a slight separation of the lateral fibres. The muscle insertion covers a long area of the maxilla, being tendinous anteriorly and musculose posteriorly. Muscle A2 is large with a deep concave anterior border.

The *levator arcus palatini* is a small thin element lying posterodorsally to the *adductor*. The *adductor arcus palatini* is divided, the anterior part inserting on the palatine, the posterior on the medial rim of the hyomandibula.

Summary and discussion of the muscles associated with the jaws and suspensorium

Certain features of these muscles are common to all macrouroids, namely:

1. Muscle A1 is never separated by A2, as is the case in other gadiforms and divisions A1 α and A1 β lie in the same vertical plane.
2. Muscle A1 β always lies lateral to the ramus mandibularis of the trigeminal nerve and, because of this relationship, is homologous with that muscle in other gadiforms.

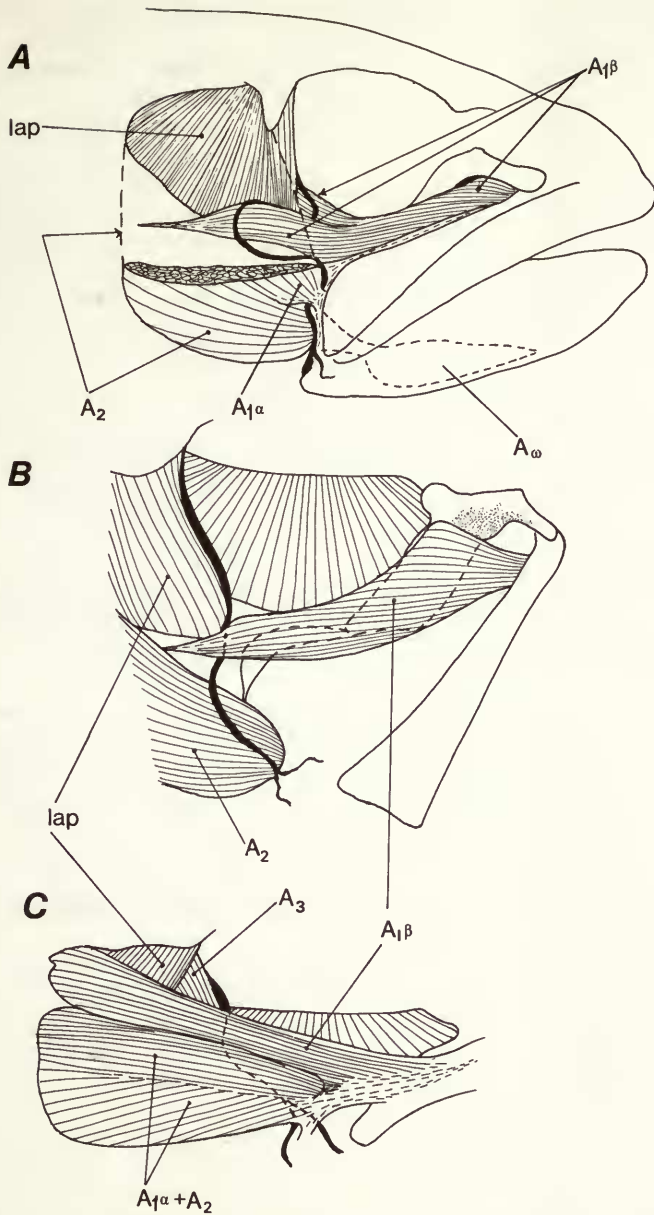


Fig. 23 Muscle $A_{1\beta}$ and its associations in: A, *Ophidion rochei* (muscle $A_1 + A_2$ cut away, its borders indicated by dashed lines; B, *Glyptophidium macropus*; C, *Lycodes frigidus*.

3. Muscle $A_{1\beta}$ never originates from the palatine, in contrast to the condition in some gadoids.
4. Muscle $A_{1\beta}$ in the majority of macrouroids, is not constricted below the orbit, nor has it an anterior expansion.
5. The *adductor arcus palatini* is continuous and never divided as in some gadoids.
6. The *levator arcus palatini* lies lateral to muscle A_1 and A_2 , a feature shared with some gadoids but few other teleosts.
7. Muscle A_3 is absent, in contrast to most other gadiforms and acanthopterygians.

Because of the often contrasting conditions in these features between macrouroids and other gadiforms, it is necessary to examine each in detail.

1. In macrouroids both muscles $A1\alpha$ and $A1\beta$ always lie lateral to muscle $A2$ and the division between the $A1$ element is in the vertical rather than the sagittal plane.

In the Macrouroidinae (*Macrouroides* and *Squalogadus*) and some genera of Macrourinae (Type II morphotype, see p. 12), $A1$ is undivided, or incompletely so. Incomplete separation of $A1\alpha$ and $A1\beta$ occurs in some gadoids (i.e. *Bregmaceros*, *Euclichthys*, *Lyconus*, *Steindachneria*, *Lepidion*). In other paracanthopterygians (ophidioids, zoarcids and percopsids) there is no $A1\alpha$, the single muscle inserting on the lower jaw. However, it is questionable whether this muscle is the homologue of $A2$ since the ramus mandibularis of the trigeminal nerve runs medial to it, and in some taxa the upper portion of the muscle has a close association with the maxillo-mandibular ligament. For example, in the ophidiiform *Ophidion rochei* (Fig. 23A) the ramus mandibularis runs medial to the upper part of the muscle, which is attached to the maxillo-mandibular ligament, the nerve then piercing the element and running laterally into the lower jaw. In the zoarcid *Lycodes frigidus* (Fig. 23C) the entire length of the nerve branch runs medial to the outer muscle bloc, but there is a distinct lateral myocomma which marks an abrupt change in fibre direction; the dorsal, parallel fibres insert directly onto the maxillo-mandibular ligament. In the percopsiform *Percopsis* (Fig. 24), although the nerve runs medial to the outer adductor muscle, there is no sign of any fibres running onto the maxillo-mandibular ligament or the upper jaw.

Thus, on the basis of the position of the ramus mandibularis and on what has been said above (p. 16) concerning its topographical position, the outer muscle in the above mentioned ophidioids, zoarcids and percopsids must be construed as the homologue of the element identified as $A1$ in macrouroids and gadoids (and various other teleosts) despite the fact that in some cases it does not insert on the upper jaw.

Whether the lack of an upper jaw insertion is the plesiomorphic condition or whether attachment of the muscle to the upper jaw has been lost, may only be assessed through congruence with other synapomorphies.

In the majority of acanthopterygians the ramus mandibularis of the trigeminal nerve consistently lies medial to muscle $A1$ (and so by its position signifies the identity of that element) even though in some taxa it follows the anterior border of $A2$.

2. Muscle $A1\beta$ (and $A1\gamma$). A brief account was given above (p. 16) of the nomenclatural history of muscle $A1\beta$ and it is now treated in detail.

Rosen (1973), realised, correctly, that the muscle in question is not the homologue of the *levator maxillaris superioris* of halecomorphs, which muscle comprises several sections having their origins from the infraorbitals and lateral ethmoid as well as from the palatine and hyomandibula.

In macrouroids muscle $A1\beta$ lies lateral to the ramus mandibularis and in some taxa it is incompletely separated from $A1\alpha$ posteriorly. It always inserts on to the medial face of the maxillary shaft and is never attached to an element of the suspensorium.

In assumed primitive gadoids (Bathygadidae; see Howes, 1988), muscle $A1\beta$ has a similar morphology to that in macrouroids and similarly lies in the same vertical plane as muscle $A1\alpha$. However, in progressively more advanced gadoids $A1\beta$ shifts medially; in *Melanonus* and *Steindachneria* the shift concerns only the anterior part of the muscle, but in the Euclichthyidae and other gadoids (apart from the Bregmacerotidae) the posterior part of $A1\beta$ also shifts medially so that the entire muscle comes to lie mesiad not only to $A1\alpha$, but also (in more advanced gadoids) to $A2$.

In the Trachyrincidae although there is a single adductor muscle, it has a double insertion on the maxilla (p. 17) suggesting that $A1\alpha$ and $A1\beta$ are fused. According to Casinos (1978) *Trachyrincus* has lost muscle $A1\alpha$ and it has been 'replaced' by a '... displacement outwards of the levator maxillae superioris' (i.e. $A1\beta$). There is, however, no evidence to suggest that such a loss and subsequent displacement has occurred. On the contrary, I would advocate that the opposite is the case and that muscle $A1\beta$ has shifted medially in gadoids (see above). The situation in *Trachyrincus* is simply a derived specialisation of that taxon.

Casinos (*op. cit.*) in studying a limited taxonomic range of macrouroids has failed to take into

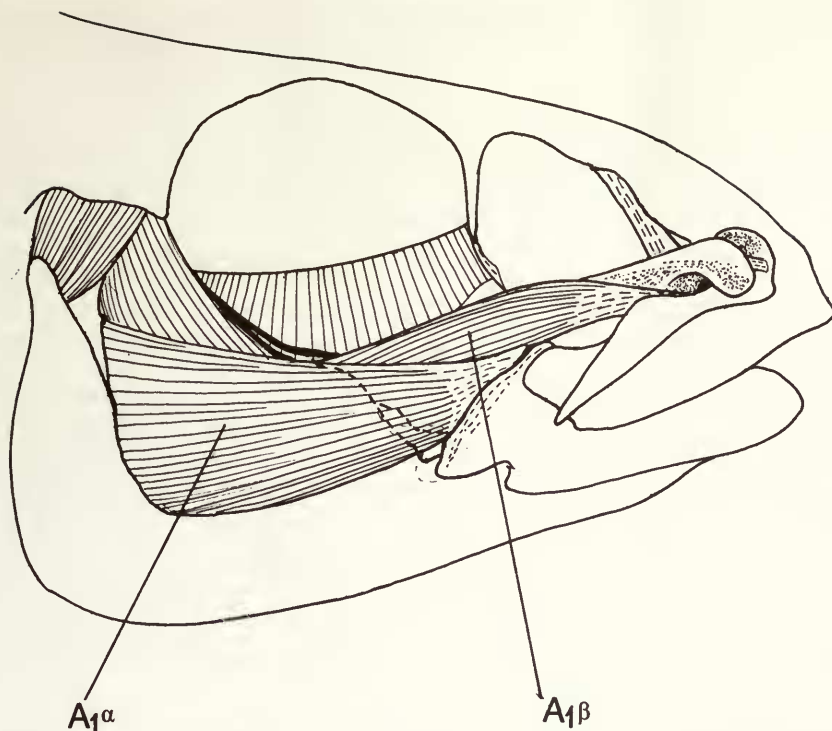


Fig. 24 *Percopsis omiscomayus*. Upper jaw and suspensorial muscles in lateral view. Medial pathway of ramus mandibularis indicated by dashed lines.

account the varying morphology of the adductor muscle. A single element also occurs in the Macrouroidinae and in a group of macrourines (see p. 13), and is probably also the result of fusion between A1α and A1β.

Lauder & Liem (1983: 148) state that it is only in more advanced paracanthopterygians that muscle A1β alone inserts on the maxilla. These authors do not justify that statement by providing examples, nor do they include it as a synapomorphy in their cladogram of paracanthopterygians. Accepting their statement means that no gadiform can be considered 'advanced'. But, on the basis of this character ophidiiforms and percopsiforms must form a monophyletic assemblage. If lophiiforms are taken to be 'advanced paracanthopterygians' then Lauder & Liem's hypothesis is rejected because muscle A1β is absent in these fishes (muscle A1 is a single element inserting on a broad ribbon-like maxillary tendon and posteriorly is undifferentiated from A2).

As noted above, in macrouroids and gadoids muscle A1β lies lateral to the ramus mandibularis of the trigeminal nerve. In other paracanthopterygians, however, the muscle lies medial to the nerve. A variation of this condition is illustrated in the ophidiiform *Ophidion rochei* where the nerve loops medially around the muscle's origin on the hyomandibula (Fig. 23A). In another ophidioid, *Glyptophidium macrops*, the nerve also passes medially to A1β, but A1α is lacking (Fig. 23B). In the neobythitine ophidiiform *Lamprogrammus niger* the ramus mandibularis follows a convoluted path. In this taxon the outer muscle bloc comprises two elements, the dorsal of which inserts on the maxillo-mandibular ligament and the ventral on the mandible. There is a well-developed A1β which is divided posteriorly by the *levator arcus palatini* muscle. The mandibularis nerve passes between the divisions of A1β, then medially to the dorsal adductor element. The nerve then runs laterally across the upper part of the ventral adductor segment, after which it turns inward to course medially to the lower segment. Thus, using the nerve pathway as the criterion of muscle identification, not only is the upper segment A1α, but so is the ventral portion of the lower segment,

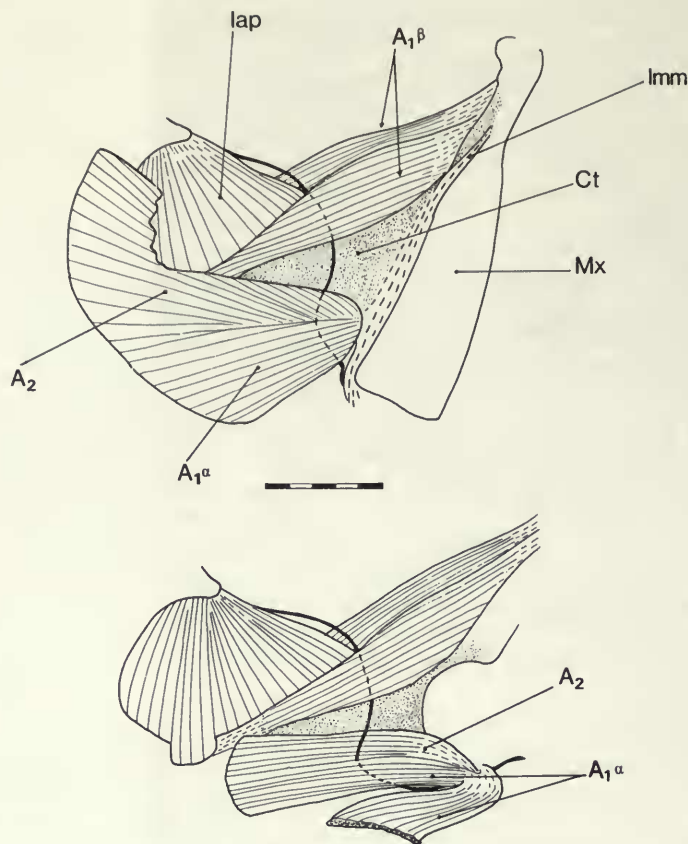


Fig. 25 *Lamprogrammus niger*. Muscle $A_1\beta$ and its associations. In A the upper part of muscle A_2 is cut away, and in B the superficial part is removed with $A_1\alpha$ reflected.

despite its insertion on the lower jaw. Muscle A_2 is that small dorsal portion of the lower segment inserting on the mandible (Fig. 25).

Muscle $A_1\beta$ is reported to occur widely in neoteleosts; according to Lauder & Liem (1983: 143) it occurs in stomiiforms, some acanthopterygians, some paracanthopterygians and some aulopiforms but not in atheriniforms or neoscoelids. This statement appears, in part, to be based on the work of Rosen (1973). According to Rosen (*op. cit.*) there is, in stomiiform fishes, an $A_1\beta$ and sometimes an $A_1\alpha$. Fink & Weitzman (1984) maintained that $A_1\beta$ was a neomorphic feature independently derived in stomiiforms, myctophiforms and acanthomorphs (Fig. 26C). I agree that $A_1\beta$ in gadiforms is not homologous with the so-called $A_1\beta$ in stomiiforms or myctophiforms, nor indeed with that in lower groups in which it has been reported (e.g. halosauran elopomorphs; Greenwood, 1977). My reasoning for this assumption is that in those latter groups the muscle in question always lies medial to the ramus mandibularis of the trigeminal nerve (see for example Tchernavin, 1953, fig. 29). In higher neoteleosts an $A_1\beta$ muscle is recorded by Rosen (1973) in some beryciforms. He notes that stephanoberycids have entirely separate internal and external maxillary muscles similar to the gadiform condition. However, I find that in *Stephanoberyx monae*, an example illustrated by Rosen, muscles he labels as A_2 and $A_1\beta$ are united at their origin (Fig. 26B). Rosen's $A_1\beta$, which in his figure appears to have a double insertion on the maxilla, is equivalent to my $A_1\alpha$, and his $A_1\alpha$ corresponds to the upper part of what I interpret as muscle A_2 since this element inserts on the lower jaw; as shown in Rosen's figure. In the beryciform *Hoplostethes*, muscle A_1 lies laterally to A_2 (Fig. 26A).

In the myctophiforms examined (*Lampanyctus*, *Electrona*) and that illustrated by Rosen (1973), (*Protomyctophum*), only an $A1\beta$ is present and this also lies medial to the ramus mandibularis branch of the trigeminal nerve.

Lauder & Liem's (1983: 143) statement that muscle $A1\beta$ is absent in atheriniforms needs confirmation. In the small sample examined I find that in some taxa (e.g. *Orestias*) the mandibularis nerve branch passes medially to a segment of adductor muscle which inserts on the lower jaw. This could be muscle $A1\beta$ having secondarily acquired a mandibular insertion. In *Hemiramphus* muscle $A1$ appears to be entirely lacking. If the presence of $A1\beta$ is an acanthomorph synapomorphy then its absence in various atheriniform lineages must be viewed as derived losses.

In *Polymixia* the arrangement of adductor muscles is complex (Fig. 27B). Rosen (1973: 420) suggested that the polymixiid pattern was '... transitional between the $A1$ and $A1\beta$ systems'. My interpretation is somewhat different, however, since the specimen of *Polymixia nobilis* examined differs from that of *P. japonica* illustrated by Rosen. The principal lateral muscle of *P. nobilis* appears to be a combined $A1\alpha$ and $A2$ (Rosen's $A2$) since a group of fibres inserts via a narrow tendon on to the posterodorsal part of the maxillo-mandibular ligament and passes laterally to the ramus mandibularis nerve branch. A large anteromedial muscle, corresponding to Rosen's $A1\beta$, inserts on to the dorsal surface of the maxilla. Although adhering to the maxillo-mandibular ligament by connective tissue along most of its length, its fibres remain separated from that ligament (Rosen's figure of *P. japonica* shows them inserting on to the maxillo-mandibular ligament). As shown by Rosen, there are two sections of muscle $A1\beta$ which are separated by the course of the ramus mandibularis branch. The inner section is connected to the outer anteriorly along an internal aponeurosis which is evident laterally as a tendinous band ($Ia1b$, Fig. 27B). I am unable to locate in *P. nobilis* a muscle corresponding the Rosen's labelled $A3$ in *P. japonica*.

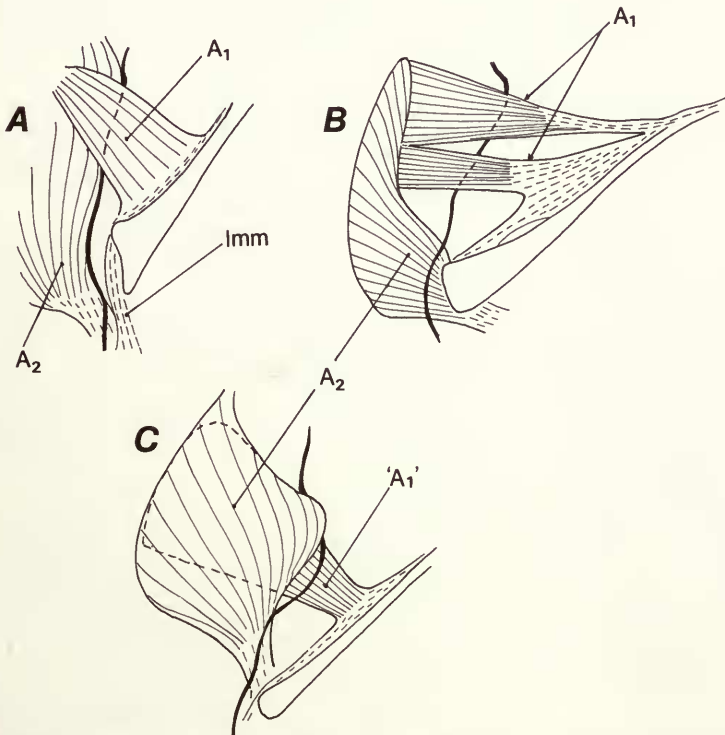


Fig. 26 The superficial upper jaw adductor musculature of the beryciformes: A, *Hoplostethes melanopus*; B, *Stephanoberyx monae*; and the stomiiform, C, *Photichthys argenteus*.

It seems that, at least in *P. nobilis*, muscle A1 β is present, although poorly differentiated, and muscle A1 β corresponds in topographical position to the so-called A1 β in myctophiforms and stomiiforms. This observation supports Stiasny's (1986) phylogenetic positioning of *Polymixia* as the sister-group of the Paracanthopterygii plus Acanthopterygii.

Rather surprisingly, the adductor muscle arrangement in the Sciaenidae (a family currently placed in Acanthopterygii) greatly resembles that of *Polymixia* and certain gadoids. In *Cynoscion* for example (Fig. 27A) muscle A1 β is divided as in *Polymixia* by the ramus mandibularis branch of the trigeminal nerve, the outer section running into the maxillo-mandibular ligament; the inner section, which originates from the quadrate and hyomandibula, also joins the maxillo-mandibular ligament for part of its length. The anterior, expanded part of the muscle originates from the palatine as in merlucciid gadoids (see above). Interestingly, Freihofer (1978: 45) draws attention to the resemblances between sciaenid and percopsiform musculature, including the innervation pattern.

One group of macrouroids, designated as morphotype Ia possesses an additional adductor muscle, termed A1 γ (p. 12). This muscle is usually a weak spindle-shaped element originating *via* a thin tendon from the medial face of A1 β and having a common insertion with that muscle on the maxilla. In *Abyssicola*, the tendon of origin stems from the anterior rim of the hyomandibula and in this respect resembles the condition of A1 β in certain gadoids (see above). I have not found a muscle corresponding to A1 γ in any other acanthomorph taxon and regard it as synapomorphic for the macourine genera *Coryphaenoides*, *Abyssicola*, *Nezumia*, *Coelorinchus*, *Lionurus*, *Nematonurus* and *Chalinura*.

3. *Origin of muscle A1 β from the palatine.* Among gadoids this feature occurs in the Merlucciidae (*Merluccius*, *Macruronus* and *Lyconus*). The anterior part of muscle A1 β originates from a lateral palatine cavity (complexly so in *Lyconus*; see p. 26 above). The origin of part of A1 β from the palatine also occurs in some sciaenids (see above) in which taxa it is considered to have arisen independently from that in merlucciids (see Howes, 1988 concerning the phylogenetic position of the Merlucciidae).

4. *Suborbital constriction of muscle A1 β and its insertion.* There is no suborbital constriction of muscle A1 β in macrouroids. In gadoids, however, a tendinous constriction of the muscle occurs in the Bathygadidae, Moridae, Melanonidae (*sensu* Howes, 1988) and Euclichthyidae. Constriction of the muscle below the orbit leads to an anterior expansion of the muscle.

The occurrence of a suborbital constriction of the dorsal part of A1 in such unrelated groups as Cichlidae (Otten, 1981) and Cyprinidae (Howes, 1984a) casts doubt on the feature having any phylogenetic significance; it seems to be a functional means of accommodating the eye. That this is so is indicated by the long and obliquely angled jaws of the gadoid taxa possessing the constriction, which necessitates a sharp change in angle to pass around the eyeball. In contrast, the jaws of macrouroids are short, so that the fibres of muscle A1 β are directed downward and their course is uninterrupted by the eye. The Trachyrincidae are exceptional in that although possessing long jaws they are horizontally aligned and the muscle remains unconstricted (Fig. 7), although the eye is not relatively smaller than that in macrouroids.

Although in primitive gadoids such as *Bathygadus* and *Gadomus* (Figs 9 & 11) the anterior 'expansion' of muscle A1 β follows as a consequence of suborbital constriction, in more advanced gadoids this expansion has apparently a functional nature in that it is bulbous and transversely expanded, and fills the palatine cavity; in merlucciids this section of the muscle is even attached to the palatine (see p. 12). Thus, I have considered the anterior development of muscle A1 β to be a synapomorphy for gadoids including and above *Bathygadus* (Howes, 1988).

The variability of the site of attachment of muscle A1 β to the maxilla demands some comment. In macrouroids the anterior part of the maxilla bears a prominent ventromedial process which contacts the ascending process of the premaxilla (Mvp, Figs 2 & 3). On the inner side of the maxillary ventral process is a small depression into which inserts the tendon of A1 β (Fig. 28A). A similar ventromedial process occurs in the Bathygadidae and Moridae but is not so well-developed

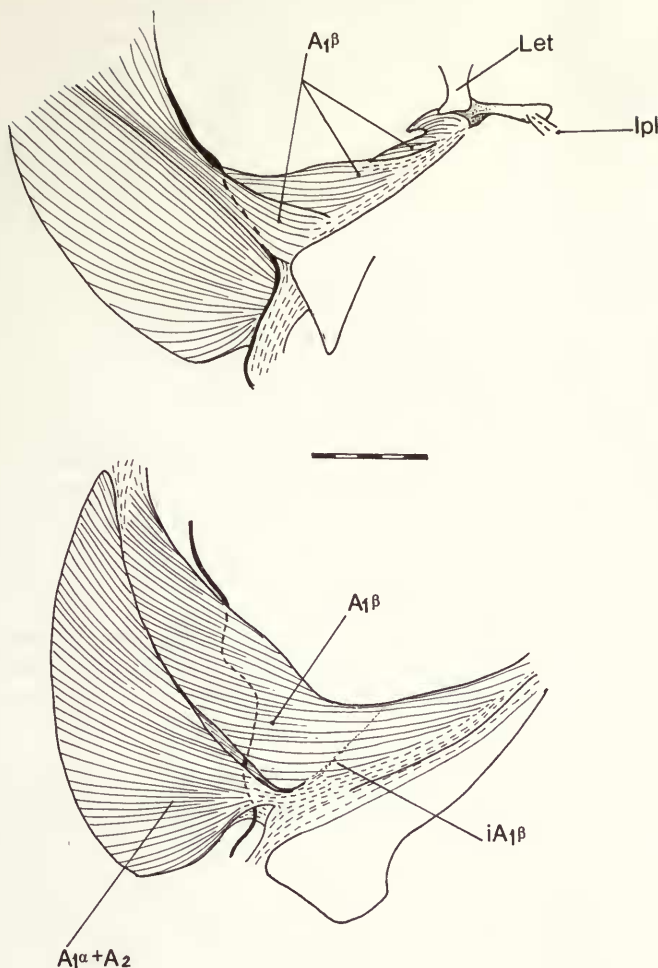


Fig. 27 Jaw adductor muscles in A, a sciaenid *Cynoscion jamaicensis* and B, a polymixiid *Polymixia nobilis*.

as that in macrouroids and the tendon of $A1\beta$ inserts on the posterior rim of the ventromedial process (Fig. 29A).

In the Trachyrincidae, the inner insertion tendon (presumably representing $A1\beta$; see above, p. 17) inserts on the dorsal aspect of a medial maxillary shelf (Fig. 29B). This is similar to the situation in other gadoids where the muscle insertion is shifted forward to insert along the dorsomedial ledge of the maxilla (e.g. Euclichthyidae). In the Melanonidae and Merlucciidae $A1\beta$ inserts on the medial aspect of the maxillary head (Fig. 29C) whereas in the more advanced gadoids (Gadidae, Lotidae, Phycidae, Ranicepsitidae, Muraenolepididae; see Howes, 1988) its insertion is on the ventral limb of the maxillary head (Fig. 29D).

The anterior shift of $A1\beta$ insertion appears to be correlated with the transverse expansion of that muscle and its shift from a lateral to medial position with respect to the outer adductor muscle (see above). It is supposed that the anterior placement of the muscle's insertion site is a derived condition for those families listed above.

5. The *adductor arcus palatini* is, in some gadoids divided into anterior and posterior parts. According to Winterbottom (1974a: 238) the *adductor arcus palatini* in its plesiomorphic state is

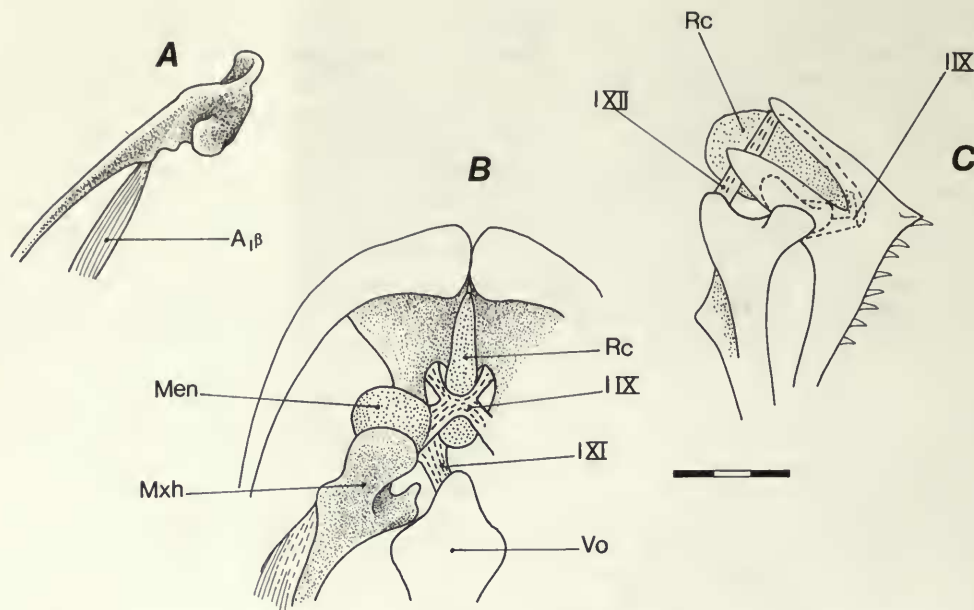


Fig. 28 A, *Nezumia hildebrandi*, insertion of muscle $A_{1\beta}$ on maxilla (ventral view); B, *Coelorinchus caribbaeus*, ventral view of maxillary and premaxillary ligamentous connections; C, *Ventrifossa occidentalis*, lateral view of maxillary-premaxillary-rostral cartilage associations.

confined to the posterior region of the orbit between the skull and hyomandibula; its derived condition is to floor the orbital cavity and extend posteriorly. Part of the *adductor* in gadoids usually originates from the parasphenoid, only a small portion stemming from the prootic; a separate *adductor hyomandibulae* is not recognisable. The division of the *adductor arcus palatini* in some gadoids (*Bregmaceros*, *Macruronus*) is, on the basis of in- and out-group distribution, a derived condition and a 'precursor' can be recognised in some morids (p. 20) and *Steindachneria* (p. 22) where the central portion of the muscle is thin and weakly developed.

Apart from *Bathygadus*, *Gadomus* and *Euclichthys* an anterior insertion of the *adductor arcus palatini* on to the palatine is a feature of all gadiform fishes examined, and is also present in some ophidiiforms. Among acanthopterygians a palatine attachment of the *adductor arcus palatini* is present in Sciaenidae, Eleotridae and some Cichlidae (see, for example, Greenwood, 1985). Of other families checked for this feature, it is lacking in Pomacentridae, Labridae, Atherinidae, Nototheniidae, Stephanoberycidae, Polymixiidae, Scombridae, Sparidae and Lutjanidae. Admittedly this is not an exhaustive survey of acanthopterygian taxa but it does not indicate that a palatine attachment of the *adductor arcus palatini* is an unusual acanthopterygian condition; such an attachment has been treated as derived (Greenwood, 1985: 156; 165). To treat a palatine attachment of the *adductor* as a synapomorphy uniting the majority of gadiforms and some ophidiiforms, would conflict with the pattern of relationships arrived at through other synapomorphies (see Howes, 1988). It is more parsimonious to assume an independent derivation of the feature in the various lineages in which it occurs.

6. In the Trachyrincidae, the *levator arcus palatini* is extensive posteriorly, covering the upper part of the plate-like preoperculum and lying medial to A1 (Fig. 7). In the Melanonidae and Steindachneriidae the *levator* is small, its insertion being high on the preopercular limb (Figs 12 & 13). A similar situation occurs in the Bregmacerotidae, where the *levator* is much reduced and inserts on the dorsal margin of the preoperculum (Fig. 22), a feature also present in the percopsiform *Percopsis* (Fig. 24).

The Euclichthyidae has an autapomorphic arrangement of the *levator arcus palatini*. Although extensive, the muscle does not lie laterally to the superficial adductor musculature as in lower gadoids and macrouroids, but mostly posteromedial. Near its insertion the *levator* is bifurcate, the posterior segment inserting on the preoperculum and just overlapping the posterodorsal edge of A1, the anterior one inserting on the hyomandibula and joining an aponeurosis from which originates muscle A1 β (Fig. 14).

The morphology of the *levator* in *Euclichthys* could, in evolutionary terms, be construed as the 'precursor' of the situation found in other gadoids where the entire muscle lies medial to the outer part of the *adductor mandibulae*.

If the acanthomorph condition of the *levator arcus palatini* occurring medially to the outer adductor muscle be regarded as the plesiomorphic condition, then the similarly placed muscle in higher gadoids is a phylogenetic reversal from the laterally placed *levator* which characterises the macrouroids and majority of gadoids. One may then interpret as 'intermediates' between these taxa and higher gadoids the posterior shifts of the *levator* found in the Melanonidae and Bregmacerotidae and partial lateral overlap of the adductor in the Euclichthyidae.

7. *Muscle A3 is lacking in macrouroids.* This muscle is usually defined as the most medial of the adductor complex, having its insertion in the lower jaw (according to Winterbottom 1974a: 234) on the 'medial face of the dentary, in the Meckelian fossa, or both.' Allis (1897: 581) identifies the A3 as that muscle lying medial to the adductor ramus of the maxillaris inferioris nerve.

In most acanthomorphs, the ventral fibres of A3 converge with those of A2 on to a common aponeurosis which attaches to the inner face of the anguloarticular. Dorsally, A2 and A3 are separated by the *levator arcus palatini*. In macrouroids and many gadoids, the *levator* lies outside the adductor complex (see above) and so the medial adductor bloc comprises a single element dorsally. Only in the more advanced gadoids (*Gadus*, *Lota* etc.) is it possible to distinguish an A3 on the grounds of its dorsal separation from A2 by a *levator arcus palatini*. In macrouroids and lower gadoids, the insertion of the medial adductor element (A2) on the lower jaw is a simple one; all fibres converge into an aponeurosis from which departs a ventrally directed tendon. The tendon inserts on the coronomeckelian bone; no fibres are associated with the tendon.

In advanced gadoids the situation is more complex, with the inner fibres of A2 inserting on the coronomeckelian tendon, while those of A3 cross over to insert on the lateral tendinous sheet.

According to Casinos (1978) muscle A3 in gadoids is homologous with the inner part of the macrouroid adductor complex. Furthermore, Casinos regards the gadoid (= my higher gadoids, e.g. *Gadus*, *Merluccius*, *Pollachius*) condition of separate A2 and A3 muscles to be plesiomorphic

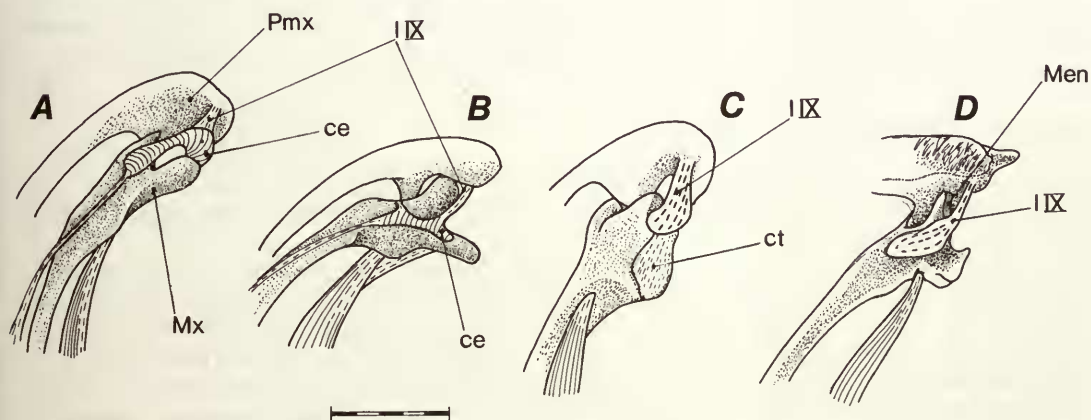


Fig. 29 Maxillary insertion of muscle A₁ β and the ligamentous connection between the maxilla and premaxilla in: A, Bathygadidae, *Bathygadus favosus*; B, Trachyrincidae, *Trachyrincus trachyrincus*; C, Melanonidae, *Melanonus zugmayeri*; D, Gadidae, *Gadus morhua*.

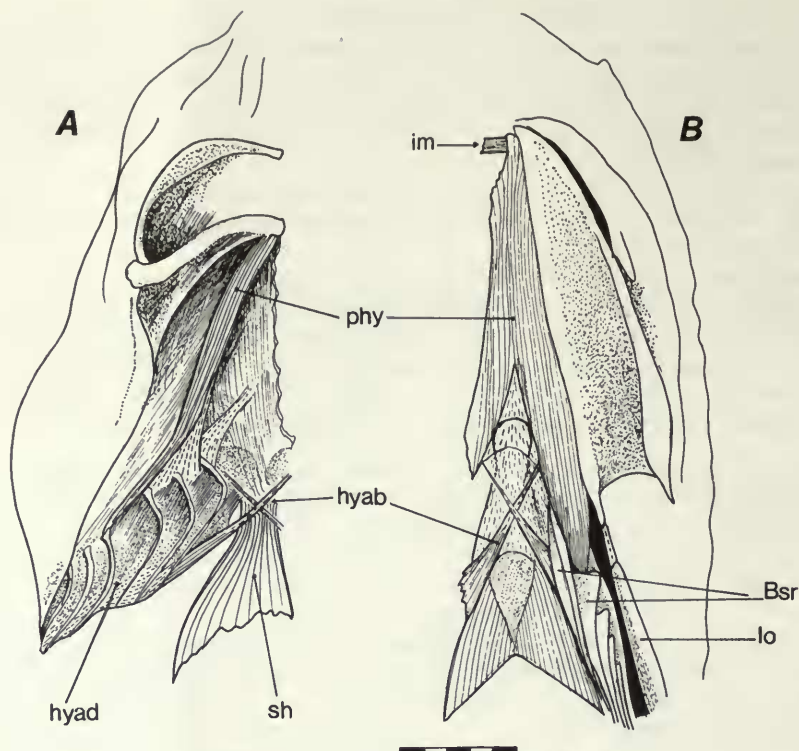


Fig. 30 Hyoid musculature of A, Macrouroidinae: *Squalogadus modificatus*; B, Macrourinae: *Coryphaenoides mexicanus*. Ventral views.

and to have given rise to derived states in macrouroids either by the amalgamation of A2 and A3 or the loss of A2.

Casinos' assumptions are based on the recognition of the gadoids as being plesiomorphic but on the contrary they appear to be the derived sister-group of macrouroids (see Howes, 1988). I would suggest that the 'amalgamation' of A2 and A3 in macrouroids (and in out-groups) is the plesiomorphic state representing an undifferentiated muscle bloc. The differentiation of a medial muscle element (A3) is a derived condition that has undoubtedly occurred independently in several teleostean lineages.

Muscles of the hyoid region

Among macrouroids there is little variability of the hyoid muscles, such variation as does occur concerns the points of attachment of the *protractor hyoidei* and the degree of development of the *hyohyoidei abductores*.

The *protractor hyoidei* originates from the anterohyal at the articulation of, and usually attaching to the 2nd, 3rd or 4th branchiostegal ray. Most frequently the muscle attaches to the proximal stem of the 3rd and 4th rays. Only in *Lionurus* is there a single attachment to the 2nd branchiostegal ray. The *protractor hyoidei* is usually well-developed. In most taxa the left and right parts of the muscle continue forward, narrowly separated from one another in the midline. Anteriorly the parts diverge slightly to insert on their respective dentary. *Echinomacrurus* is unusual among the Macrourinae in having a ribbon-like protractor hyoidei with the right and left parts separated in the midline. In this respect, *Echinomacrurus* resembles taxa of the Macrouroidinae. In both macrouroidine genera the *protractor hyoidei* is a rope-like element extending from the anterohyal

anterior to the articulation of the 4th branchiostegal ray; insertion is close to the symphyseal tip of the dentary (Fig. 30). The left and right parts of the muscle are separated for their entire lengths. In *Cetonus* the left and right parts of the *protractor* meet only beneath the ventral hyoids, remaining separated for the remainder of their lengths.

An *intermandibularis* is present in all taxa examined with a single exception, namely the macrouroidine *Squalogadus*. The muscle is a thin, narrow band of fibres with the *protractor hyoidei* inserting below it.

The *hyohyoidei abductores* run from the 1st branchiostegal ray to insert tendinously on the contralateral dorsohyal.

The *hyohyoidei adductores* are weakly developed in all taxa and usually comprise a few widely spaced fibres arranged in narrow bands connecting the branchiostegal rays (Fig. 32). Posteriorly, those fibres connecting the last branchiostegal ray with the suboperculum and operculum are stronger and more numerous.

In gadoids the hyoid musculature is generally more strongly developed than in macrouroids. For example, in the Muraenolepididae (Fig. 31), the *protractor hyoidei* is well-developed, attaching to the base of the 3rd and the upper part of the 2nd branchiostegal ray; an anterior segment of the muscle attaches tendinously to the ventromedial border of the dentary. The parts of either side meet in the midline and run forward as a single muscle inserting at the symphysis beneath a small *intermandibularis*. The *hyohyoidei abductores* and *adductores* are also well-developed.

The morphology of the hyoid muscles in the Gadidae, Lotidae and Phycidae is similar to that in the Muraenolepididae except that the *intermandibularis* is more strongly developed in the former. Holmquist (1911) has described and figured the hyoid musculature of *Gadus* in which he identifies two sections of the *intermandibularis*. Winterbottom (1974a: 245) concluded that the anterohyal section should properly be referred to as the *protractor hyoidei*.

The morphology of the hyoid musculature is rather uniform and the often recognised taxonomic grouping of macrouroids based on the number of branchiostegal rays, viz. 6 or 7 is not reflected by different muscle morphotypes. The most noticeable differences are those between the Macro-uroidinae and Macrourinae where in the former the two parts of the *protractor hyoidei* are ribbon-like and separated in the midline and the *intermandibularis* is absent (at least in *Squalogadus*). A similar separation of the *protractor* also occurs in the macrourine, *Echinomacrurus* (see above). The osteology of *Echinomacrurus* is unknown, but its external morphology would indicate that it is a

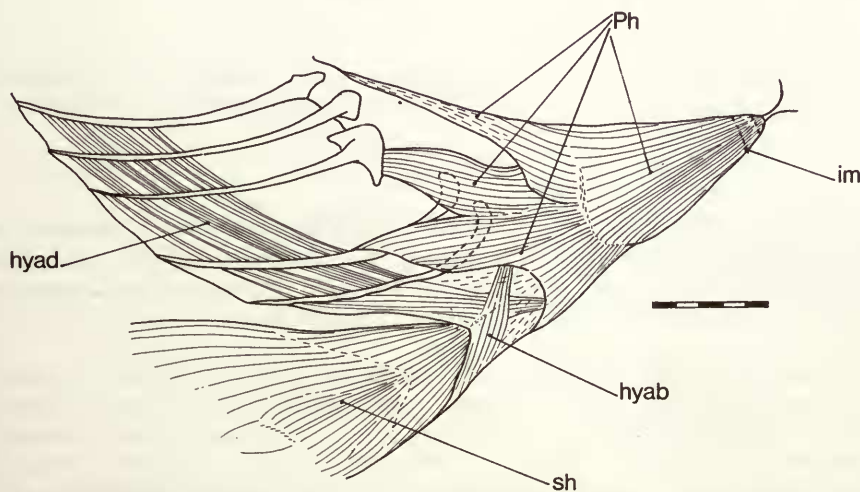


Fig. 31 Hyoid musculature of *Muraenolepis microps*; ventrolateral view, position of *intermandibularis* indicated by dashed lines.

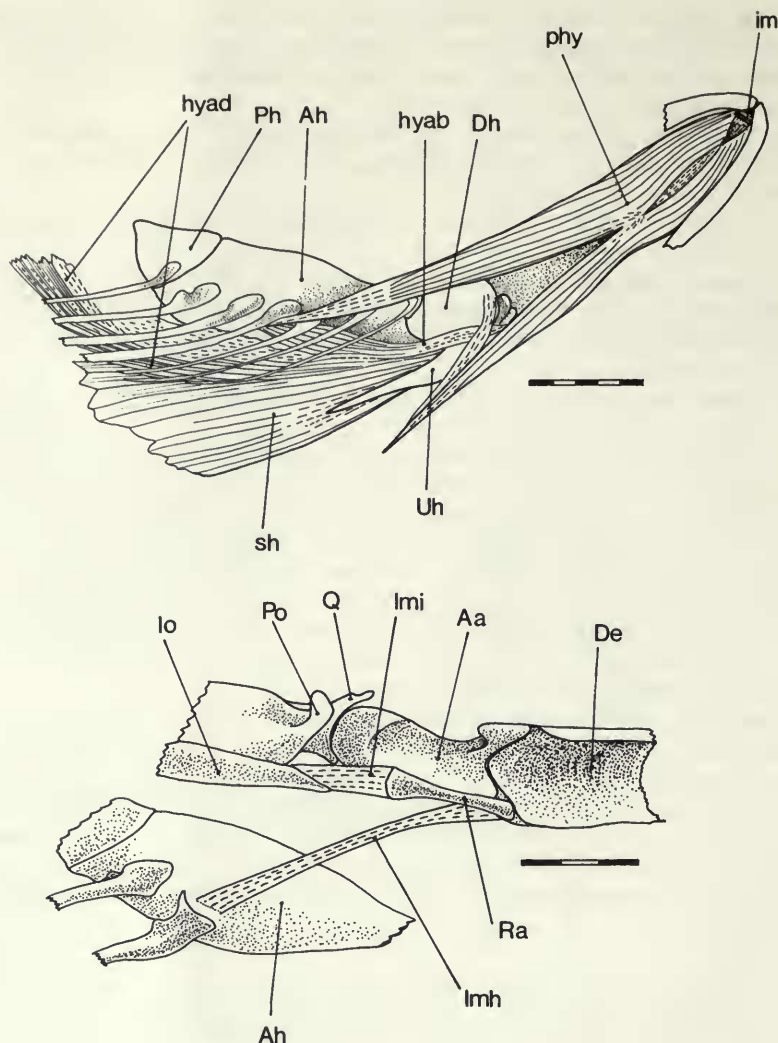


Fig. 32 *Trachyrincus trachyrincus*: above, hyoid musculature seen in oblique ventrolateral view; below, ligamentous connections of the lower jaw and hyoid bar seen in ventral view.

member of the Macrourinae, although a highly derived one. The similarity in the morphology of its hyoid muscles with that of the macrouroidines has possibly been independently derived. The complete separation of the *protractor hyoidei* in the midline is an unusual feature amongst teleosts and is known elsewhere only in the otophysan Loricariidae (Howes, 1983) and the Gyrinocheilidae (pers. obs.).

The *sternohyoideus* muscle, connecting the pectoral girdle with the hyoid bar occurs among gadiforms in two conditions—long and compressed or deep, broad and short. Usually, a long, compressed *sternohyoideus* attaches to a urohyal whose posterior margin is widely separated from the cleithrum, whereas a short, broad *sternohyoideus* is associated with a urohyal whose posterior border is in contact with, or narrowly separated from the cleithrum. The posterior limit of the *sternohyoideus* is usually well-defined ventrally by its attachment to the cleithra, but its lateral fibres are continuous with those of the body musculature (*obliquus inferioris*).

In macrourids a long, compressed *sternohyoideus* occurs in *Odontomacrus*, *Hymenocephalus*, *Chalinura*, *Echinomacrus*, *Cynomacrus* and *Lionurus*. A stout, broad muscle is present in *Macruorus*, *Nezumia*, *Trachonurus*, *Malacocephalus* and the macrouroidine, *Squalogadus*. The latter is unusual in possessing a stout *sternohyoideus* associated with a urohyal that is widely separated from the pectoral girdle, a feature also possessed by the Trachyrincidae.

Among gadoids, the Bathygadidae and Moridae have a long compressed *sternohyoideus*. However, in bathygadids the tendons of the paired *infracarinalis anterior* stretch forward from the pelvic girdle to attach via connective tissue to the ventral tips of the cleithra, and continue forward into the ventral body of the *sternohyoideus*. The tendons of the *infracarinalis* finally insert on either side of the urohyal keel (Fig. 35).

In other gadoids a long compressed *sternohyoideus* is present in the Merlucciidae where there is a well-defined ventral division of the muscle to which the *infracarinalis anterior* is tendinously linked.

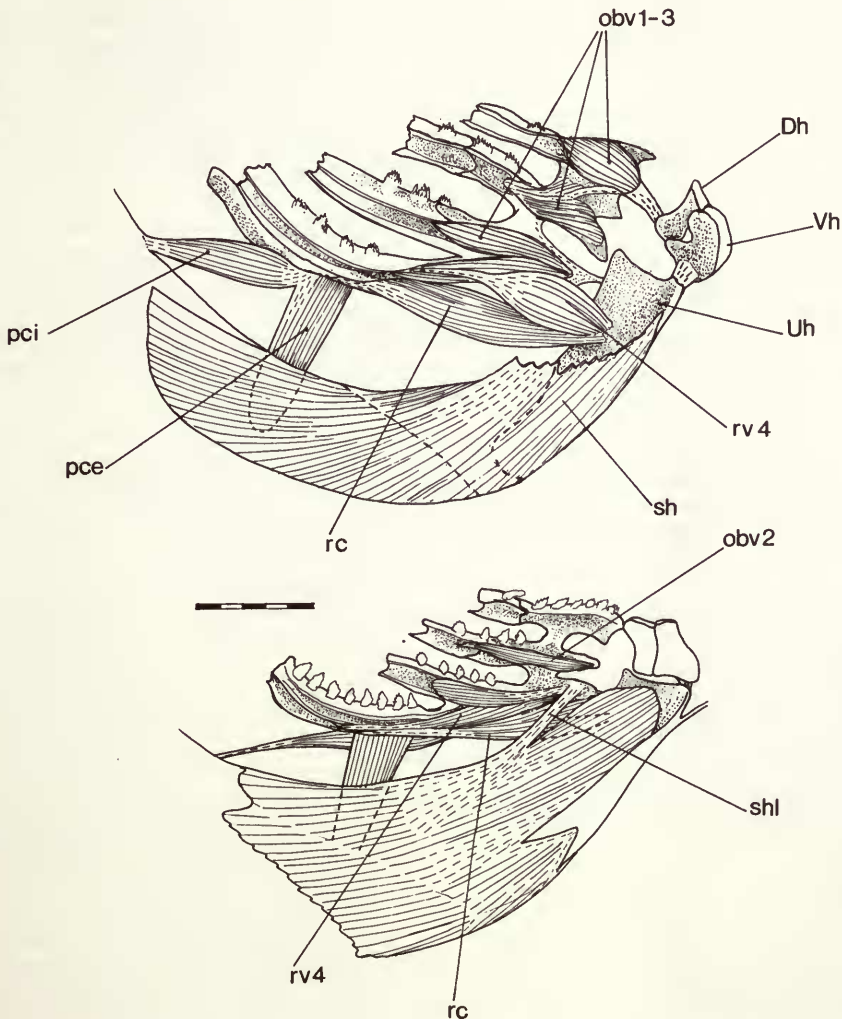


Fig. 33 Ventral gill-arch musculature of: A, a macrourid, *Macrourus berglax*; B, a gadoid, *Trachyrincus trachyrincus*. Ventrolateral views. In A the anterior border of the cleithrum is indicated by a dashed line.

In all gadiforms and other paracanthopterygians examined a dorsolateral segment of the *sternohyoideus* inserts on a stout tendon which runs anterodorsally to insert on the 3rd hypobranchial (see Figs 33–36). In acanthopterygians (?all) a similar tendon runs from the dorsomedial part of the muscle.

Ventral gill-arch muscles

Macrouroids, in common with almost all teleosts possess well-developed *obliquus ventrales* on the 1st through 3rd ventral gill-arches (Fig. 33A; 34). In contrast, gadoids have reduced (or even lack) *obliquus ventrales* on either the 1st or the 1st and 2nd gill-arches (Fig. 35). The Bathygadidae, Steindachneriidae, Melanonidae, Moridae and Trachyrincidae have reduced (or in some bathygadids lack) the muscles from only the 1st arch (Figs 33B; 34); see Howes, 1988. Reduction takes the form of a tendon attaching to the proximal tip of the ceratobranchial and with only a minute muscular element being present. In the Bregmacerotidae, the muscles appear to be lacking entirely on the 1st and 2nd gill-arches.

Winterbottom (1974a: 263) notes that there are a variable number of *recti ventrales* in teleosts. The usual acanthomorph condition is for *rectus ventrales* IV to run between the semi-circular ligament connecting the 3rd hypobranchials across the midline, and the 4th ceratobranchial. This is also the condition present in the majority of macrouroids, with the exception of *Hymenocephalus* where the anteroventral part of the muscle inserts on the urohyal and in *Macrourus*, where the entire muscle inserts on the bone. *Squalogadus* is also exceptional in that the *rectus ventrales* IV joins posteriorly to the tendon of the *rectus communis* and so by-passes the 4th ceratobranchial, inserting instead on the 5th.

Among gadoids, the *rectus ventrales* IV attaches to the urohyal in *Lyconus* (Merlucciidae), the Ranicepitidae, Phycidae and Muraenolepididae. In other merlucciids, Bathygadidae, Moridae, Steindachneriidae, Melanonidae and Lotidae, the muscle attaches together with the *rectus communis* to a dorsal aponeurosis of the *sternohyoideus* muscle (Fig. 35). In the merlucciid *Macruronus*, the *rectus ventrales* IV has a long tendon which inserts on the 5th ceratobranchial; the muscle itself is separated from the 4th arch, and anteriorly attaches to a complex aponeurosis of the *sternohyoideus* (Fig. 36).

Table 2 Insertion sites of *rectus communis* and *rectus ventralis* IV muscles in macrouroids and gadoids. Uh = urohyal; Sh = sternohyoideus; 3Hy = third hypobranchial

	<i>Rectus communis</i>		<i>Rectus ventralis</i> IV		
	Ur	Sh	3Hy	Sh	Uh
Macrourinae					
(a, majority)	*		*		
(b, 5 genera)		*	*		
(see Table 1)					
Trachyrincidae		*	*		
Bathygadidae		*	*		
Moridae		*	*		
Euclichthyidae		*	*		
Merlucciidae		*		*	*(<i>Lyconus</i>)
Melanonidae	* and 3Hy		*		
Steindachneriidae		*		*	
Gadidae		*	*		
Phycidae (part)	*				*
Phycidae (part)		*	*		
Muraenolepididae	*				*
Ranicepitidae	*				*
Lotidae		*		*	

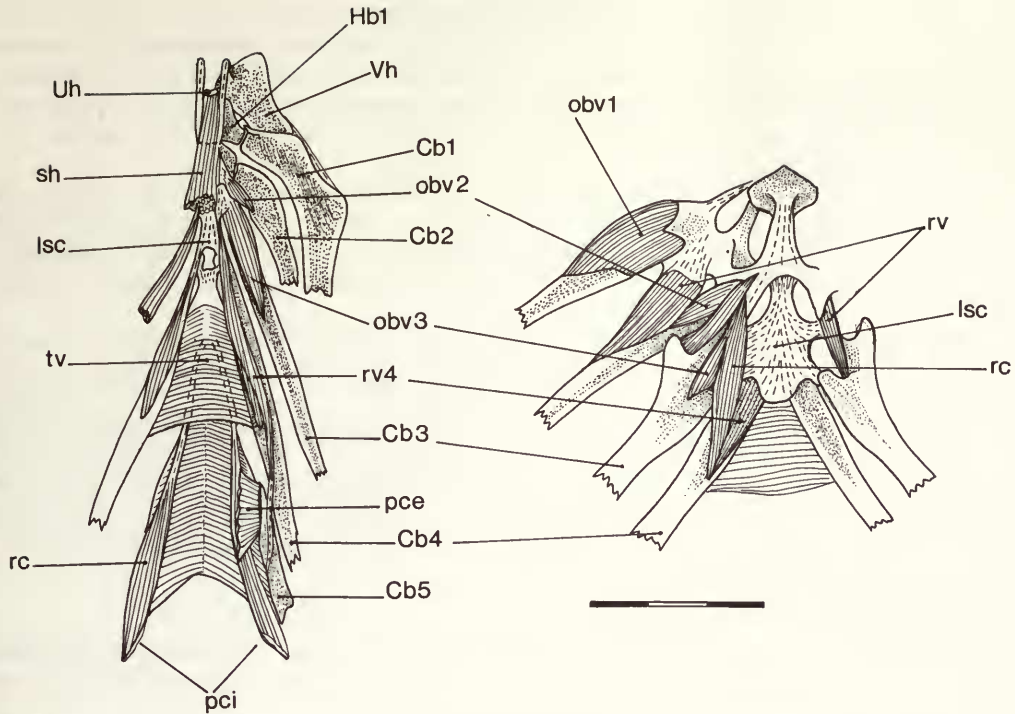


Fig. 34 Ventral gill-arch musculature of: A, a gadoid, *Bathygadus melanobranchus*; B, a macrouroid, *Nezumia hildebrandi*. Ventral views.

In other paracanthopterygians examined, *rectus ventrales* IV extends from the 3rd hypobranchial ligament to the 4th ceratobranchial, namely, the plesiomorphic acanthomorph condition.

In nearly all macrouroids, as in the majority of acanthomorphs, the *rectus communis* runs from the urohyal to the 5th ceratobranchial. Exceptional taxa are *Nezumia*, *Ventrifossa*, *Hymenocephalus*, *Odontomacrus* and *Cynomacrus*, where the *rectus communis* runs from a dorsal tendon of the *sternohyoideus* to the 5th ceratobranchial.

Among gadoids, the *rectus communis* almost always has a direct attachment to the *sternohyoideus*; in some taxa the *rectus communis* joins a tendinous aponeurosis (Merlucciidae, Fig. 36); in others, the fibres run into the body of the *sternohyoideus* and insert on an internal myocomma (Trachyrincidae, Fig. 33); and yet others, the *rectus communis* attaches directly to the urohyal (some Phycidae, Ranicepitidae, Muraenolepididae and Lotidae). However, unlike the condition in macrouroids and acanthomorphs it attaches to the anterior tip of the bone rather than to the lateral face of the keel. This different insertion site on the urohyal suggests that the attachment has been secondarily derived to that in acanthomorphs rather than representing a plesiomorphic condition (see Howes, 1988).

The various conditions of ventral gill-arch muscles in macrouroids and gadoids are summarised in Table 2.

Lauder (1983) considered a urohyal attachment of the *rectus communis* a synapomorphy for the ctenosquamates (Myctophiformes, Paracanthopterygii and Acanthopterygii). Because of its urohyal attachment, Lauder prefers the term '*pharyngohyoideus*' for ctenosquamates rather than *rectus communis*. I have, however, continued the use of *rectus communis* for gadoids since here there is no, or at best, an indirect urohyal insertion. It could be argued that '*pharyngohyoideus*' should be used for macrouroids, but here too there are exceptions to a urohyal insertion (see above and Table 2).

Following Lauder's assumption that a urohyal attachment for the *rectus communis* is a derived state it would appear that a direct linkage with the *sternohyoideus* represents a further derived condition. If it be assumed that this condition represented a less derived state, i.e. an evolutionary 'intermediate' position between a hypobranchial and urohyal attachment then it must also be assumed that the gadoids are less derived than myctophiforms, a conclusion unjustified on the basis of other synapomorphies (see Lauder & Liem, 1983).

Howes (1987) considered the *rectus communis*-*sternohyoideus* linkage to be a synapomorphy uniting gadoids. It is now apparent that the feature also occurs in some macrouroids (see above). The possession by macrouroids of other synapomorphies lacking in gadoids makes it reasonable to assume, however, that the *rectus communis*-*sternohyoideus* linkage in the five macrouroid genera (see p. 47) is homoplastic.

Lauder (1983: 26) notes that in euteleosts a *rectus ventralis* IV commonly originates from the urohyal, but that the muscle is mosaically distributed and has probably evolved independently in several lineages through the subdivision of the *rectus communis*.

The lability of the *rectus ventralis* IV casts doubt upon its usefulness as a phylogenetic indicator and I have preferred to regard its association with the *sternohyoideus* in the Moridae, Merlucciidae and Lotidae as having been derived independently in those lineages; certainly there are no other synapomorphies that would suggest a close relationship of these taxa (see Howes, 1988). Further discussion of functional aspects of the ventral gill-arch musculature is given on pages 54–55.

Dorsal gill-arch muscles

Unlike the ventral gill-arch musculature, there is little variability in the dorsal gill-arch muscles among macrouroids apart from the angles at which the *levator*s are aligned between the gill-arches and the cranium, and in the size differences of some muscles.

The basic pattern present in all macrouroid and gadoid taxa examined is: three *levatores externi*, two attaching to the 1st and 2nd and the third to the 4th epibranchials (*levator* IV crosses the otic region of the cranium anteroventrally, medial to *levatores* I and II); two *levatores interni*, one attaching to the 2nd infrapharyngobranchial, the other to the 3rd or 4th (Fig. 37); all these muscles originate from the intercalar and/or the upper part of the prootic.

Transversi dorsales run from the 2nd, 3rd and 4th epibranchials to a midline raphe (that serving the 2nd and 3rd arches is a single element); an *obliquus posterior* connects the postero-medial surface of the 4th epibranchial with the 5th cerato-branchial (pharyngeal tooth-plate).

In macrouroids the *retractor dorsalis* stems from the 3rd and 4th centra to insert tendinously on the medial rim of the 3rd pharyngobranchial. In some taxa, e.g. *Nezumia* (Fig. 38C), a ventral part of the *retractor* inserts on the rim of the 4th pharyngobranchial tooth-plate.

Lauder (1983) noted that in the gadoid *Pollachius*, the *retractor dorsalis* inserts on both pharyngobranchials 3 and 4; I find similar sites of insertion in all 'advanced' gadoids, but in merlucciids, melanonids, morids and bathgadids the muscle inserts, as in most macrouroids on the medial rim of pharyngobranchial 3.

In the Muraenolepididae, the *retractor dorsalis* inserts only on pharyngobranchial 4 (Howes, 1988). Lauder's (1983) and my own observations on acanthopterygians suggest that insertion on pharyngobranchial 3 is the plesiomorphic site of attachment and that one involving the 4th pharyngobranchial is the derived state. In this respect, the Muraenolepididae is the most derived group of gadoid taxa.

Eye muscles

Macrouroids and gadoids lack a posterior myodome, apparently a secondary loss (see Patterson, 1975: 544). The posterior eye muscles originate from a medial septum close to the floor of the parasphenoid and run almost lateral to their insertions on the eyeball. The accompanying figure of *Gadomus* (Fig. 39) exemplifies the condition in all macrouroids and gadoids examined (the eye muscles of *Gadomus* are narrower than in most other taxa). In some gadoids the posterior eye muscles originate from a small ossified protruberance of the parasphenoid. In *Gaidropsarus*,

Merluccius and *Brosme* the eye muscles pass medial to a vertical parasphenoid-pterosphenoid strut bordering the optic fenestra.

The origin of the posterior eye muscles from the centre of the parasphenoid and their transverse orientation is considered a further synapomorphy uniting the Macrouroidei and Gadoidei (see Howes, 1988).

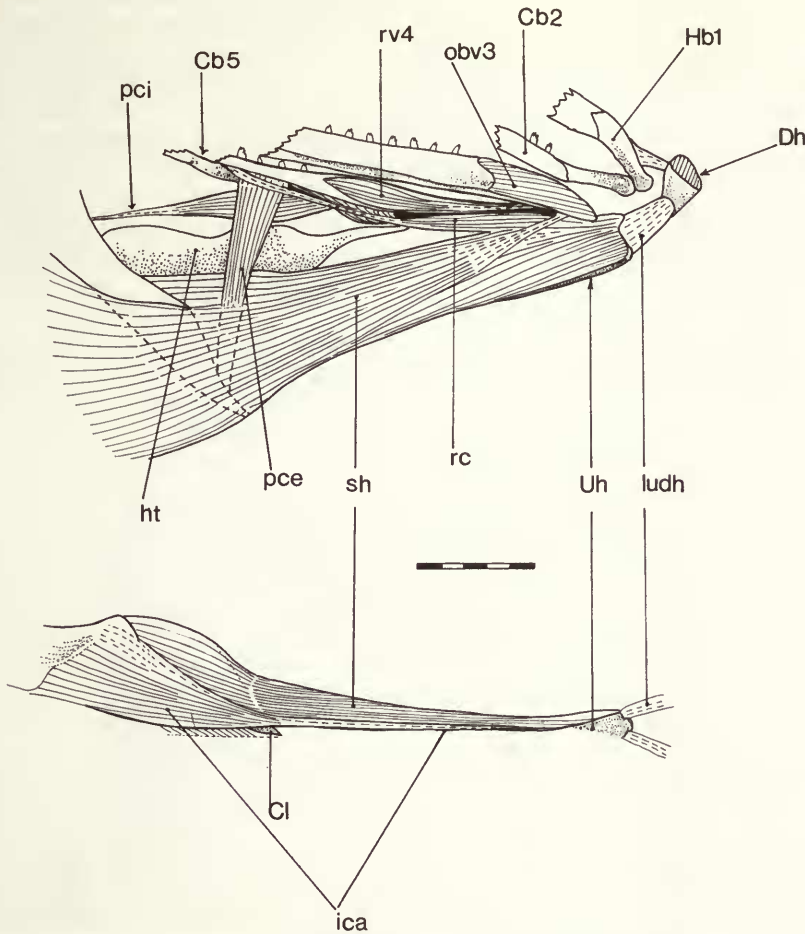


Fig. 35 Ventral gill-arch and hyoid muscles of a gadoid, *Gadomus longifilis*. Above, lateral; below, ventral view.

Functional and ecological inferences

Jaw protrusion mechanisms

Recent recoveries of live macrouroids (Wilson & Smith, 1985) while encouraging, also indicate the difficulties of maintaining these fishes under laboratory conditions. Results so far discount the possibility of obtaining direct experimental data on jaw function. One is therefore obliged to derive hypotheses of functional mechanisms from morbid anatomical investigation.

Those who have studied macrouroid anatomy are agreed that the jaws of most taxa are highly protrusible, the degree of protrusibility being a corollary of the length of the premaxillary ascending process (Okamura, 1970*a,b*; Marshall & Iwamoto, 1973: 479; Geistdorfer, 1975; McLellan, 1977;

Casinos, 1978; 1981). Several models of acanthomorph upper jaw protrusion mechanisms have been proposed, but most authors are in agreement that muscle A1 plays a predominant part in this function (see Lauder, 1982: 280; Motta, 1984 for references to, and review of previous literature). Rosen (1973) disagrees, however, believing that the development of an A1 α or A1 β division of the *adductor mandibulae* '... is not dependent on, or even correlated with, the existence of a protrusible jaw mechanism ...'.

According to Anker (1974) muscle A1 serves not only to keep the mouth closed but possibly forces protrusion of the premaxilla. Gosline (1981: 15) thought the most likely cause of jaw protrusion in acanthomorph fishes is ligament IX, viz. that connecting the rostral cartilage with the maxilla. He hypothesised that as the maxilla twists around its articulation with the cranium, it pulls ligament IX anteroventrally, thus protruding the premaxilla which is attached to the rostral cartilage. This idea does not entirely explain protrusion, however, since the initial twisting of the maxilla must be explained in terms of muscular control. Is the maxilla pulled downward and inward passively by abduction of the lower jaw, or through direct action of muscles A1 α and A1 β ?

McLellan (1977) accounted for upper jaw protrusion in macrouroids by the action of muscle A1, since she found that pulling on the maxillo-mandibular ligament along the line of force exerted by

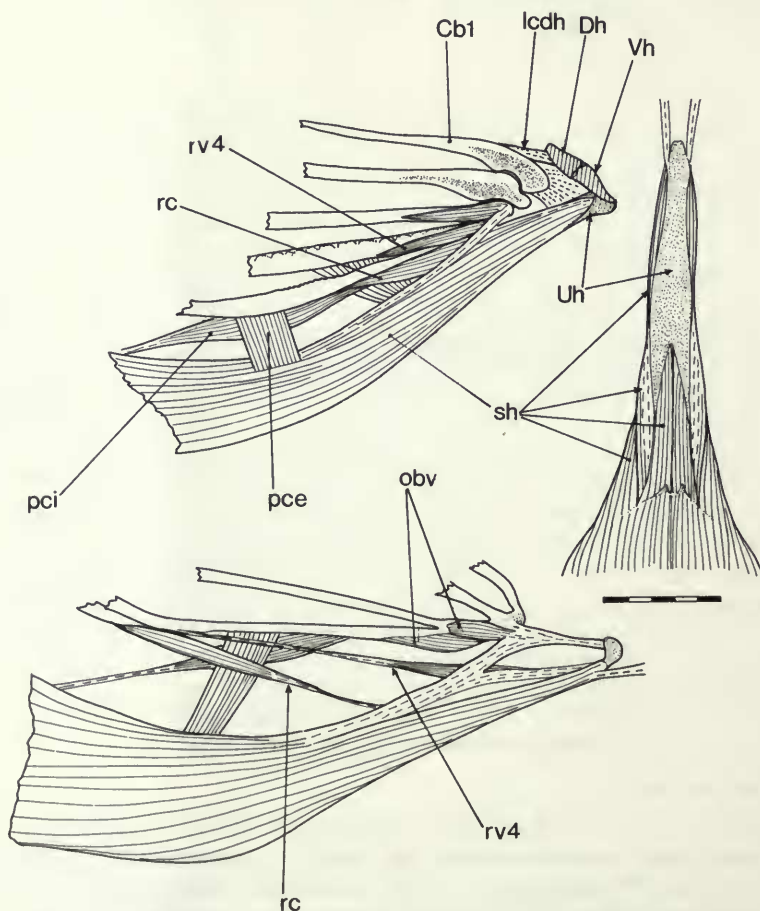


Fig. 36 Merlucciidae; ventral gill-arch and sternohyoid muscles of *Merluccius merluccius* in A, lateral and B, ventral views; the latter showing the partitions of the *sternohyoideus*. C, *Macruronus magellanicus* in lateral view.

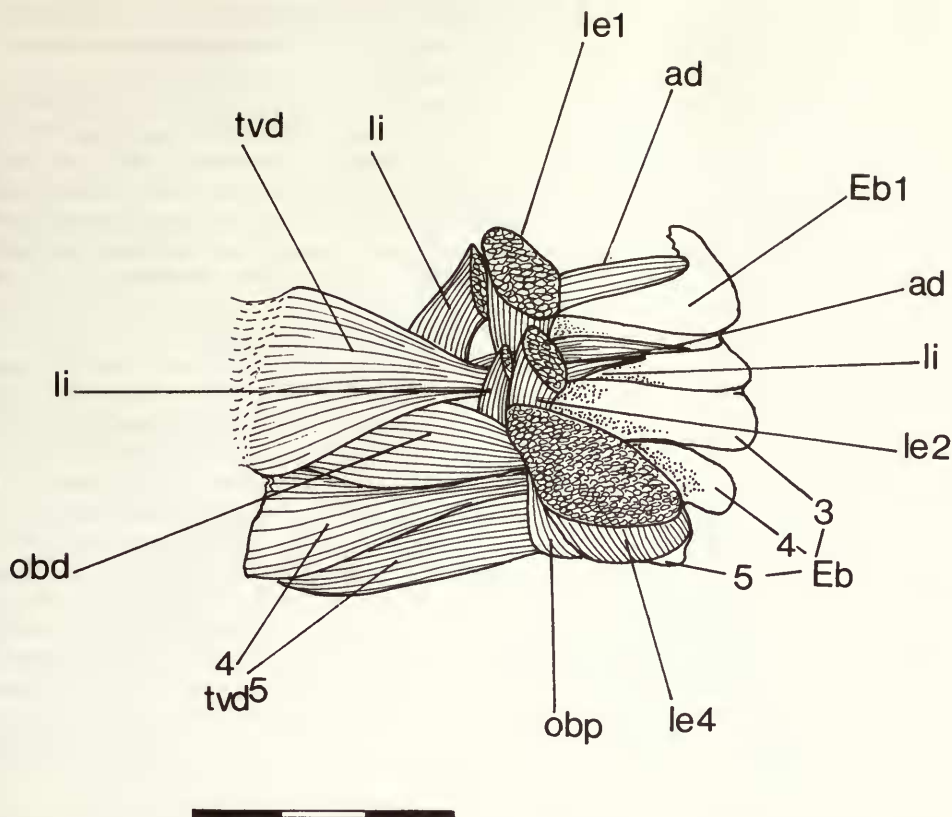


Fig. 37 Dorsal gill-arch muscles of a macrourid, *Coelorinchus caribbaeus* (dorsal view).

the fibres of A1 produced premaxillary protrusion. However, McLellan hypothesised that the macrouroid type of mechanism was '... a fundamentally different means of protruding the upper jaw from that of *Bathygadus*', which she supposed to be produced by rotation of the maxillary head (i.e. as in Gosline's hypothesis).

Geistdorfer (1975) gave a theoretical account of jaw movements in the macourine *Ventrifossa occidentalis*. For the most part, he considered jaw action to be similar to that in acanthopterygians and although stating that protrusion is limited by ligaments, he gave no account of arthrology.

Casinos (1981) attempted an explanation of jaw protrusion in gadids (Gadidae) based on observation by high-speed cinematography, and in macrouroids by the extrapolation of these data. According to Casinos, there is no or little jaw protrusion in gadids, except *Pollachius*, whereas there is pronounced protrusion in macrouroids.

Casinos devised a protrusion index (not to be confused with the protrusion index of Okamura, 1970b; see below) which showed that although the gadid *Pollachius* has a high degree of protrusion, comparable with that of macrouroids, the 'macrouroid' *Trachyrincus* has a low protrusion index comparable with that of the gadids.

Casinos' explanations of these apparent anomalies are confusing and rely on different sizes and moments of muscle A1 β , and are also based on incorrect anatomical data. For example, Casinos explains the higher degree of protrusibility in macrouroids as due to an 'additional' rostro-maxillary ligament. However, a rostro-maxillary ligament (ligament VII, see p. 6) is present in *all* gadiforms and indeed all acanthomorphs (Stiassny, 1986).

I would agree with Casinos (1981) that the restriction of muscle A1 β to the same vertical plane as A1 α gives the macrouroid upper jaw a degree of freedom greater than that of gadoids where the

vertical movement of the maxilla appears to be restricted by the obliquely and transversely angled $A1\beta$ (particularly so in merlucciids where a short-fibred $A1\beta$ runs from the palatine to the maxillary head thus affording the maxilla little downward movement).

As noted above (p. 38) in some gadoids, seemingly those with restricted jaw protrusibility, the insertion of $A1\beta$ is sited further anteriorly on the maxilla than in those with a greater degree of jaw freedom. In macrouroids the insertion of muscle $A1\beta$ is on the ventromedial prominence posterior to the maxillary head. As noted above (p. 39) in gadoids the ventromedial process is less prominent and in more advanced taxa is reduced to a medial shelf, with the insertion of $A1\beta$ shifted anteriorly to what is regarded as the most derived situation, namely to the symphyseal border of the maxillary head. It was also noted above (p. 39) that the anterior insertion of $A1\beta$ is correlated with the medial shift and enlargement of the entire muscle.

What is possibly an important factor concerning differences in protrusion between macrouroids and gadoids is that in macrouroids muscle $A1\alpha$ is attached to the maxilla *via* the maxillo-mandibular ligament (Figs 1–4), whereas in gadoids $A1\alpha$, although often associated with the maxillo-mandibular ligament is fastened to the jaw independently by its own tendon (Figs 9–20).

Another factor which may affect the degree of protrusibility is the ligamentous connection between the maxillary head and the premaxillary ascending process. It was noted above (p. 7) that there are different forms of attachment between these bones in gadoids. The ligament (lig. XI) either attaches directly to the bone or *via* a cylindrical chondroid or fibrous element. The latter form of attachment (confined to the more plesiomorphic gadoids) suggests a greater degree of separation between the bones. In macrouroids the meniscus is a thick disc, loosely interposed between the maxillary head and the premaxilla, with ligament IX also attaching to the rostral cartilage (Fig. 28B & C). Thus, the only check on a total downward release of the premaxilla is ligament XI, which connects the maxilla to the ethmoid. If this ligament is cut in preserved specimens, there is a dramatic and passive jaw protrusion. Such is not the case in gadoids where muscle $A1\beta$ runs obliquely from the suspensorium to the maxilla and acts as a brake, but there is a pronounced protrusion in those gadoids where $A1\beta$, like the macrouroids, lies in the same vertical plane as $A1\alpha$ (e.g. *Bathygadus*, *Gadomus*). Thus, it is suggested that muscle $A1\beta$ plays an active role in both holding and rotating the maxilla and so effecting protrusion of the premaxilla as hypothesised by Alexander (1963) and Gosline (1981).

A further point to be considered is that suggested by Casinos (1981) concerning the role of the labial 'ligament' (see p. 8). In Casinos' view in macrouroids the '... depression of the lower jaw transmits the force by means of the circumbuccal ligament' (=labial ligament). Since a labial ligament is also highly developed in some gadoids (*Bathygadus*, *Melanonus*, *Merluccius*) presumably the same function applies in these taxa. Casinos' statement is somewhat ambiguous, however, particularly as he regards the ligament as extending around the mandibles whereas in fact, there is a separate ligament attached to each dentary (see Fig. 9). Nonetheless, the idea that the ligament plays a role in protruding the upper jaw appears valid when one considers the direct linkage of the ligament from the mandible to the premaxilla and maxilla and that it appears to be a contractile element (see p. 8). In this regard, some attention should be paid to the work of Otten (1983) who points out the importance of the maxillo-dentary, and the posterior premaxillary-maxillary ligaments in jaw protrusion.

Otten (1983) recognised two groups of acanthopterygian fishes on the basis of jaw protrusion morphotypes:

1. in which the maxilla rotates about its long axis and pushes the premaxilla anteriorly (exemplified by *Perca*).
2. in which the maxilla pushes, pulls and retains the premaxilla in protruded position (occurs in cichlids). He notes, however, that these two groups show some degree of overlap.

Otten also makes the point that a shortening and steepening of the premaxillary ascending process coupled with a caudo-ventral shift in the insertion of muscle $A1$ are factors responsible for increased biting force. Although Otten's hypotheses were directed toward cichlid jaw mechanisms, these principles also apply to macrouroids. Most macrouroids differ noticeably from gadoids in their long, steep premaxillary ascending processes and posterior insertion of $A1\beta$ (see p. 38).

Motta (1984) reviewed the history of ideas concerning the mechanics of teleost jaw protrusion and presented a classification of protrusion types but unfortunately disregarded paracanthopterygians in his account. Following Motta's classification the macrouroids and gadoids would seem to fall into three of his four categories, namely, type A: protrusion as a result of mandibular depression; type B: as a result of maxillary twist, and type C: as a result of neurocranial elevation (the degree of development of *epaxialis* musculature in many gadoids suggest this).

Motta also believes that the 'twisting maxilla model' has been overemphasised and that the 'mandible depression model' of jaw protrusion is probably the dominant type. Motta emphasised that the protruded mouth forms a circular orifice which is the most efficient configuration for employing suction feeding (see also Osse & Muller, 1980). A circular, protruded mouth profile is probably produced by all macrouroids and plesiomorphic gadoids (i.e. *Bathygadus*, *Gadomus*).

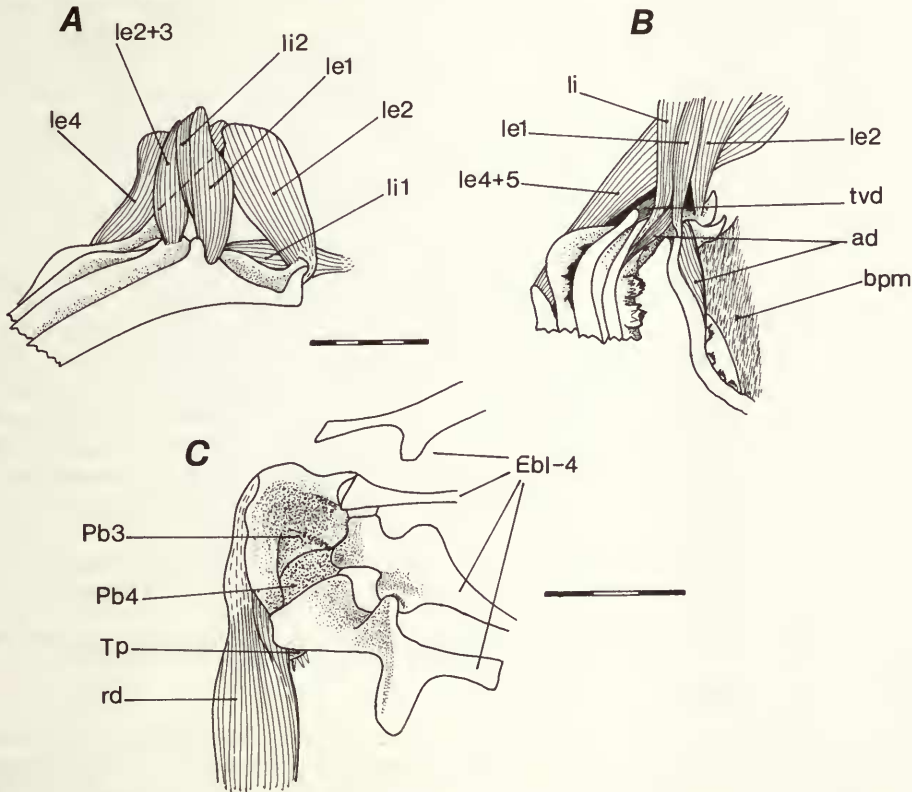


Fig. 38 Dorsal gill-arch muscles of: A, a gadoid, *Gadomus longifilis*; B, a macrourid, *Nezumia hildebrandi* (lateral views); C, *Nezumia hildebrandi* showing *retractor dorsalis* insertion (dorsal view).

Hyoid-opercular mechanisms

In discussing *Bathygadus*, McLellan (1977: 1026–7) states that '... the motion of the maxilla is mediated through a ligament of the interopercle ...' and '... ligamentous connections between the interopercle, subopercle and opercle, and the contraction of the levator operculi muscle which runs from the cranium to the opercle.'

Although the opercular series-jaw linkage serves to depress the mandible, its effect on moving the maxilla is doubtful. Furthermore, McLellan has overlooked the fact that *Bathygadus*, in

common with other gadoids, possesses a different jaw-opercular linkage system from that in other acanthomorphs (see p. 9). The interoperculum, instead of being the mediator between the mandible and suboperculum as in most acanthomorphs mediates between the mandible and preoperculum/hyomandibula. It should be noted that in most macrouroids and all gadoids the *adductor operculi* muscle inserts principally or entirely on the horizontal, opercular process of the hyomandibula; although the *levator* retains some attachment to the operculum, often its area of insertion is small and confined to the anterodorsal margin of the bone.

The *adductor operculi* normally acts as an antagonist to the *dilatator operculi* and together they elevate the operculum. The consequences of the redirection of the *adductor* force to the hyomandibula are difficult to evaluate, but a rotational component directly coupled via the hyomandibular-interopercular ligament to the lower jaw is suggested. Another feature to note is that because of the anterior shift of the *adductor operculi* and the reduced insertion area of the *levator operculi*, there is a greater medial surface area available for the insertion of the *hyohyoidei adductores*, and in the Phycidae, Lotidae and Muraenolepididae, for epaxial muscle as well (see p. 32).

The presence in the Trachyrincidae of a mandibulohyoid ligament (Fig. 32) may be another indication of this taxon's closer relationships with gadoids than macrouroids (see Howes, 1987). However, as yet, too few comparative data exist on the distribution of a mandibulohyoid ligament to comment on its phylogenetic value. It is certainly present in most, if not all basal euteleosts and has been reported in clupeomorphs, stomiiforms and percomorphs (see Verraes, 1977; Otten, 1982 for specific examples). The ligament has also been reported by Holmquist (1911) in the gadoid *Gadus*, a condition which I can confirm. Furthermore, the ligament is also present in other Gadidae examined and the Lotidae and Phycidae, but not in the Muraenolepididae.

According to Verraes (1977) a mandibulohyoid ligament is a feature of fishes having a long lower jaw and short interoperculum. In *Trachyrincus* the ligament attaches to the central part of the anterohyal (Fig. 32) but in other gadoids it attaches to the posterior part of the anterohyal as in the percomorph *Perca* (see Verraes *op. cit.*). According to Lauder & Liem (1980: 389) in the salmonid *Salvelinus* the presence of the mandibulohyoid ligament possibly allows for another coupling to depress the lower jaw. Such may also be the case in *Trachyrincus* and other gadoids where it is present. Otten (1982: 47) believes that the occurrence of the mandibulohyoid ligament in various teleosts is homoplastic. 'Undoubtedly, ligaments are products of evolutionary pathways. Theoretically, redundancies may occur along these pathways, but it is more likely that ligaments evolve together with the whole apparatus in which they are functional . . . '.

Finally, it should be noted that macrouroids and gadoids possess an elongate interhyal. Lauder & Liem (1980) drew attention to two functional roles of the interhyal in feeding mechanics, namely:

- giving the hyoid an increased dorsoventral rotation and so providing greater orobranchial expansion
- giving the hyoid a posterodorsal movement.

Although the above discussion has concentrated on the jaw mechanism in terms of feeding, the various modifications of the jaws and their couplings in gadoids possibly have a greater significance in respiratory function. After all, Smith & Hessler (1974) have pointed out that the respiratory rate for cod (*Gadus*) is over twenty times greater than that for a macrouroid (*Coryphaenoides*). Experimental and functional analytic data are needed to assess the significance of the gadoid type of lower jaw coupling in which an interopercular-preopercular-hyomandibular ligament is introduced.

Pharyngeal mechanisms

Geistdorfer (1975) described and commented on the pharyngeal dentition of various macrouroid genera but paid no attention to the pharyngeal musculature. There is little variation in both the upper and lower pharyngeal muscles in the taxa examined (see p. 48). In general the *posterior levatores* are long, deep and angled at 45°, suggesting a high degree of forward movement of the upper pharyngeal apparatus.

The functional significance of a *sternohyoideus* link with the *rectus communis* and *recti ventrales*

IV muscles is speculative. According to Lauder (1983: 25) the shift of the anterior attachment of the *rectus communis* from hypobranchial 3 to the urohyal is a key specialisation in the evolution of euteleostean pharyngeal manipulation. A urohyal attachment of the muscle provides an axial rotation to the pharyngeal tooth plates. In gadoids the degree of axial rotation allowed by a direct *sternohyoideus-rectus communis* link would seem to be minimal but might facilitate asymmetrical activity of the lower pharyngeal tooth-plates.

The reduction or absence of *obliquus ventrales* muscles associated with the 1st and/or 2nd gill arch is probably correlated with a strong ligamentous attachment of the 1st gill-arch to the hyoid bar.

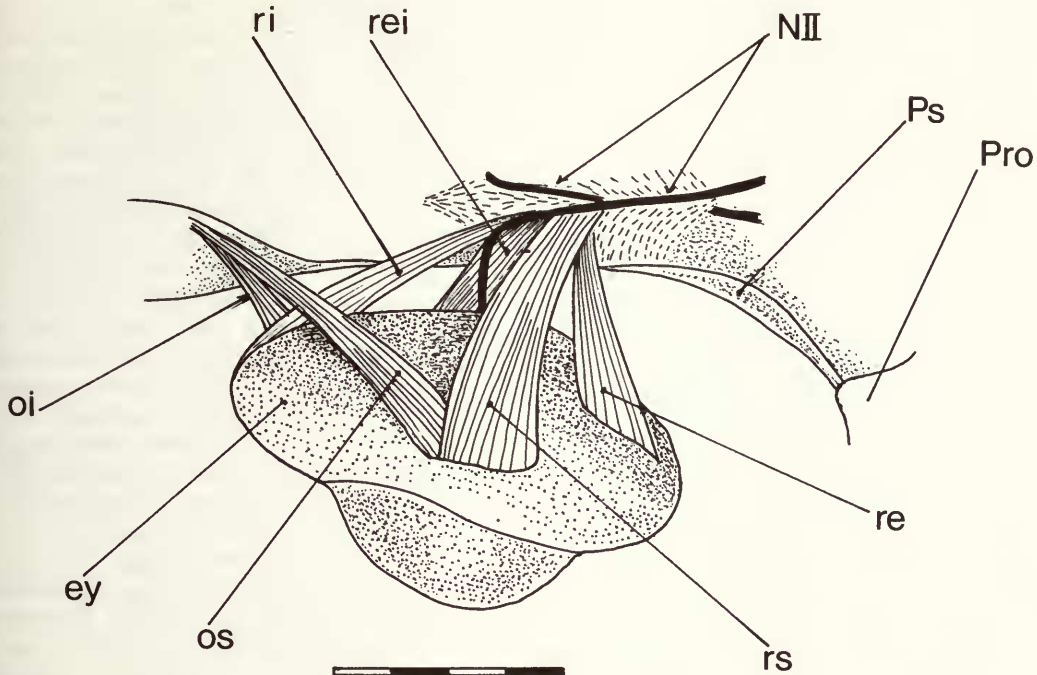


Fig. 39 Eye muscles of a gadoid, *Gadomus longifilis*. Dorsal view of left eye.

Trophic strategies

The trophic ecology of macrouroids is poorly known, but it would seem that the majority of taxa feed on a broad spectrum of organisms (see Mauchline & Gordon, 1985). This trophic diversity is a consequence of the rather unspecialised organisation of the adductor and ventral gill-arch musculature described in this text.

Okamura (1970b) classified macrouroids into four groups according to their jaw and mouth type and devised a protrusion index (a percentage ratio of premaxillary ascending process length to that of the ramus), the application of which gives a higher figure to the smaller mouth. Okamura attempted to relate the index to ecological categories, those taxa with a low index being predominantly nekton feeders, those with a high index being mostly benthic feeders. Okamura's groupings included *Bathygadus* and *Gadomus*, which are here considered to be gadoids and which according to his formula have a low protrusion index. *Trachyrincus* was not studied by Okamura, but application of his formula to this taxon gives it a protrusion index closer to *Bathygadus* and *Gadomus* than to any macrouroid.

McLellan (1977) also attempted to correlate head shape with trophic specialisations and believed she could match those taxa with long rostra (i.e. elongate nasals) to benthic habitats, whereas taxa with large, terminal mouths were associated with benthopelagic feeding. In McLellan's view *Bathygadus* and *Coelorinchus* represent two extremes of the Macrouridae with regard to ratio of mouth to head length, degree of jaw movement and expansion of orobranchial cavity. She considered *Bathygadus* to possess a prey-capture activity similar to that of 'other teleosts' with large, terminal mouths. However, as Lauder & Liem (1980: 387) point out, the feeding mechanisms of acanthopterygians (e.g. *Perca*) and basal euteleosts (e.g. *Salvelinus*) are quite different, involving different patterns of muscle activity. McLellan's reference to 'other teleosts' presumably refers to acanthopterygians, but the anatomical observations made in this text on the mode of jaw coupling in gadoids suggest that a somewhat different type of feeding pattern to that in other paracanthopterygians and in acanthopterygians might be operating.

McLellan (1977: 1034) hypothesised that *Coelorinchus* and taxa with a protracted rostrum feed by using the rostrum as a sediment probe, as did Casinos (1978) for *Trachyrincus*. McLellan argues that this method of feeding prevents rapid forward swimming necessary for creating suction. As such she sees a high degree of muscular control in varying the protrusion angle of the upper jaw (elsewhere, however, she noted that *Coelorinchus* has 'weak musculature'). McLellan's assumption that rapid swimming is the only means of generating suction is not entirely correct, however, and she seems to be confusing inertial suction and ram feeding. For example, Lauder & Liem (1980) in their study of the salmonid *Salvelinus* note that although this fish is not *primarily* a suction feeder, inertial suction is created by varying the sequence of muscle activity, i.e. the activation of the *levator arcus palatini* prior to that of the *levator operculi* and the hyoid musculature. McLellan appears to be working from similar assumptions made by Weihs (1980) that higher swimming speeds extend the suction field further forward. However, this strategy would seem applicable only to predatory fish using strike tactics rather than hovering fish sucking food from the substrate whose principal feeding method would seem more likely to be inertial suction (see Liem, 1980).

Both McLellan (1977) and Casinos (1978) have hypothesised that the rostrum of macrouroids and trachyrincids is used as a probe. Both authors have based their assumptions on the characteristic swimming mode of macrouroids, shown in Marshall & Bourne (1964) to be head down and forming an angle of approximately 45° with the substrate. Isaacs & Schwartzlose (1975) have reported, from cinematographic evidence, macrouroids thrusting into the sediment and 'throwing a cloud of sediment through the gills'. Marshall (1979) believes this method of feeding enables macrouroids to screen ooze-laden water by forcing it through the restricted first gill-slit. McLellan also supposed that the shorter snout of some species is probably more a sensory device than a mechanical probe. It should be emphasised that the rostrum is not part of the snout (i.e. ethmoid) but comprises the medially joined nasal bones which are trough-like, house many neuromasts and are fluid filled in life. Thus, a sensory function of the 'rostrum' seems a feasible idea. Casinos (1978) in his reconstruction of *Trachyrincus* probing and feeding from the substrate appears to overlook the fact that although the mouth may appear to be inferior in relation to the extended nasals, it is, in relation to the ethmoid, terminal. Furthermore, the lack of extended premaxillary ascending processes, the elongate jaws and the wide gape of the mouth (see p. 17) all point to *Trachyrincus* being benthopelagic rather than benthic in its feeding habits. Marshall & Merrett (1977: 489) point out that *Trachyrincus* '... has a marked preference for pelagic food'.

As mentioned above, macrouroids display little morphological specialisation in their jaw musculature but from their trophic diversification (see Mauchine & Gordon, 1985) it would seem that they are capable of employing some specialised feeding habits. In this respect their feeding mechanisms resemble those of cichlids recognised by Liem (1980) as being suboptimised.

The hypothesis presented here and in Howes (1988) that *Bathygadus*, *Gadomus* and *Trachyrincus* are not members of the Macrouroidei, but represent clades within the Gadoidei, negates to a certain degree the functional hypotheses advanced by McLellan (1977) and Casinos (1978; 1981). To those authors, the Macrouroidei was unquestionably a monophyletic group and so functional mechanisms identified among any of the included taxa would be considered homologous. The identification of a different jaw coupling in *Bathygadus*, *Gadomus* and *Trachyrincus* that is shared with gadoids necessitates a reappraisal of macrouroid trophic strategies.

Taxonomic and phylogenetic inferences

The results of the character analyses in this study have already been utilised in another paper (Howes, 1988) to demonstrate the paraphyletic nature of the Macroouroidei. It has been established here and in Howes (1987) that four taxa formerly recognised as macroroids, namely, *Euclichthys*, *Bathygadus*, *Gadomus*, and *Trachyrincus* share myological and arthrological synapomorphies with the Gadoidei, viz.:

- anterior expansion of the jaw adductor muscle A1
- reduction of *obliqui ventrales* on the 1st and 2nd gill-arches
- rectus communis* attaching aponeurotically to the *sternohyoideus* muscle
- possession of an interopercular-hyomandibular-preopercular ligament.

As yet, there exists no comprehensive osteological account of *Bathygadus* and *Gadomus*, and their close affinities among gadoids are obscure. Howes (1988) tentatively recognised the Bathygadidae as the sister-group to the Moridae. The basis for this arrangement is the scale pattern shared between the two families. The scales are cycloid, with a *reticulate pattern of sulci*. According to Peabody (1931) the scale pattern of *Bathygadus* '... show no affinity for the Macrouridae and could easily be classified with either or both of the other families' (i.e. Gadidae and Bregmacerotidae). In Okamura's (1970b) opinion, the 'bathygadine' scales are not secondarily derived from the ctenoid scales present in macrourids but are 'essentially primitive' and he draws attention to the '... striking resemblance to morids ... which are characterised by the reticulate structure of ridges on the exposed area'. There are, regrettably, no derived myological features shared between the Bathygadidae and Moridae, the shared myomorphology being plesiomorphic for gadoids.

The Bathygadidae was considered by Howes (1988) to represent a plesiomorphic lineage of gadoids. Work in progress has identified further synapomorphies that support the sister-group relationship of *Bathygadus* and *Gadomus* and the distinctiveness of the family (see also p. 18), but no further evidence has come to light which would suggest that the family is anything but plesiomorphic.

Trachyrincus and *Euclichthys* each represent gadoid lineages, the former being recognised as the sister-group to all other gadoids, the latter as the sister-taxon of more advanced gadoid families (Howes, 1988).

Intrarelationships of the Macroouroidei

The attrition of the Macroouroidei by the removal of the Euclichthyidae leaves a single family in the suborder, the Macrouridae. In turn, this family has been reduced by the removal of the 'Bathygadinae' and 'Trachyrincinae' to two subfamilies, the Macroroidinae and Macrourinae. The former contains two genera, *Macrouroides* and *Squalogadus*, the latter some 30 genera of diverse external morphology.

The monophyly of the Macrouridae has been discussed by Howes (1988) and is supported by three derived characters; *levator arcus palatini* muscle enlarged and lying lateral to the jaw adductor musculature; trough-like nasal bones meeting in the midline; compressed, plate-like ethmoid.

The laterally placed *levator arcus palatini* is a feature shared with the gadoids and is discussed in Howes (1988).

The nasals of macroroids are large, with a noticeable anteroventral curvature, the anterior border is often notched and the medial surface raised, contacting its partner along the midline. Enlarged, medially united nasals also occur in the gadoid family Trachyrincidae. Arguments for recognising the macroroid and trachyrincid conditions as homoplastic are given in Howes (1988).

The ethmoid region of macroroid taxa comprises a deep, vertical, plate-like bone with an expanded base capping a cartilaginous bloc. The plate-like part of the ethmoid divides the posterior borders of the nasals and the anterior borders of the frontals. The dorsal margin of the ethmoid is confluent with the dorsomedial margin of the nasals, thus forming a long crest. The identity of the ossified crest-like cap of the ethmoid is doubtful, but it is easily detached from the ethmoid (mesethmoid) cartilage and, as there is no sign of perichondral ossification, it would appear to be a rostrodermosupraethmoid.

Apart from the derived nature of the *levator arcus palatini*, which is also shared with the Gadoidei, no myological synapomorphies have been identified which corroborate the monophyly of the Macrouridae.

MACROUROIDINAE

Three myological apomorphies have been identified in *Squalogadus*, one is also known to occur in *Macrouoides* but it has not been possible, with the nature of the material available (see p. 15), to observe the other two features. These characters are:

- protractor hyoidei* entirely separated in the midline (present in *Squalogadus* and *Macrouoides*)
- intermandibularis* lacking
- rectus ventralis* IV joins *rectus communis*, by-passes and inserts on ceratobranchial 5.

Okamura (1970*b*) treated the group as a family on the basis of '... notable differences from other macroroids'. Indeed, from the characters he enumerates there is little doubt that the Macroroidinae possess a number of uniquely derived features, e.g. anterior and posterior ascending processes of the ethmoid (? rostrodermethmoid); division of the orbital fontanel; reduced, filamentous lateral ethmoid; deep 1st infraorbital; enlarged 5th infraorbital. Other features listed by Okamura (*op. cit.*) as defining the group, however, appear to be plesiomorphic, viz.: unmodified gill-rakers, unrestricted buccobranchial aperture, dorsal fin lacking spinous rays, flattened parietal, bar-like parasphenoid. It is more difficult to ascribe polarity to certain other characters, e.g. 'rostral' cartilage between ethmoid and parasphenoid (Okamura appears to confuse the rostral and mesethmoidal cartilages); lachrymal lacking ascending process (this could be a plesiomorphic condition or a reversal).

MACROURINAE

The characters given by Okamura (1970*a,b*) and Marshall (1973) as defining macrourines are, for the most part synapomorphic; they are:

- aperture between operculum and 1st gill-arch restricted by bucco-pharyngeal lining (Fig. 38B).
- olfactory bulbs lying close to nasal sac and within the nasal cavity
- spinule-bearing scales
- swimbladder (often) with drumming muscles and high number of retia mirabilia
- presence of light organs (in some taxa).

The first three characters are common to all genera, but the other two only to some (see Fahay & Markle, 1984 for generic distribution of the light organs). No myological synapomorphies have been identified that support monophyly of the group.

Within the Macrourinae three groups of genera can be distinguished on the basis of their jaw adductor muscle morphology; see pp. 12–13. These groups largely correspond with Okamura's (1970*b*) scheme of generic relationships. Okamura's *Coelorinchus* group includes *Coelorinchus*, *Coryphaenoides* and *Abyssicola* and thus corresponds to my group Ia (p. 12). He also relates the genera *Ventrifossa* and *Malacocephalus*; *Odontomacrus* and *Cynomacrus*, and *Echinomacrus*, *Cetonurus* and *Sphagemacrus*; groupings which correspond with my group II (Table I). This group, however, is probably based on symplesiomorphies.

Two groups of genera can be distinguished on the basis of their ventral gill-arch musculature, namely those where the *rectus communis* has an aponeurotic attachment to the *sterno-hyoideus* (as in gadoids) and where the muscle inserts on the urohyal. The latter group comprising the majority of macrourine taxa, the former includes *Nezumia*, *Ventrifossa*, *Hymenocephalus*, *Odontomacrus* and *Cynomacrus*. All these genera except for one (*Nezumia*) belong to the jaw muscle morphotype II.

Conclusions

The salient points to emerge from this study of macroroid and gadoid cranial muscles are:

Anatomical

The jaw adductor muscles of macroroids are, in comparison with those of other 'paracanthopterygians', unspecialised. Muscle A1 β is homologous with that so-called element in other acanthomorphs. Muscles A1 α and A1 β lie in the same vertical plane, an arrangement which seems to afford a large degree of jaw protrusion.

The arrangement of macroroid hyoid muscles are typically those of acanthopterygians, viz.: anterior attachment of the *rectus communis* to the urohyal (with the exception of five genera), *rectus ventralis* IV to the 3rd hypobranchial, and a well-developed complement of *obliqui ventrales* muscles. In gadoids, the *rectus communis* and *rectus ventralis* IV attach directly to the *sternohyoideus* and the *obliqui ventrales* are reduced on the 1st or 1st and 2nd gill-arches (in some bathygadids they are absent from the 1st arch).

In common with acanthopterygians, macroroids possess a mandibular-interopercular-subopercular ligamentous connection. In gadoids the linkage runs from the interoperculum to the hyomandibula, preoperculum or both. In both macroroids and gadoids the *adductor operculi* muscle inserts wholly, or principally on the opercular process of the hyomandibula.

Macroroids, in common with 'lower' gadoids have the *levator arcus palatini* situated postero-lateral to the jaw adductor muscles. This is considered a derived condition and one allowing for a high degree of orobranchial expansion.

Taxonomic and phylogenetic

The Macroroidae comprises a single family, the Macrouridae and two subfamilies, Macrourinae and Macroroidinae. Although the monophyly of the Macrouridae is unsupported by myological characters, the presence of a maxillary-nasal ligament and a rostral cartilage attachment of ligament IX corroborates other synapomorphies.

Monophyly of the Macroroidinae is attested by ventral gill-arch and hyoid muscle synapomorphies (pp. 43; 46). No myological characters have been identified as synapomorphic for the Macrourinae, although two jaw adductor muscle morphotypes are identified, one of which, possessed by the genera *Coelorinchus*, *Coryphaenoides*, *Abyssicola*, *Nezumia*, *Lionurus*, *Nematonurus* and *Chalinura* is considered to be derived.

Functional

Previous functional hypothesis of macroroid feeding mechanisms were based on the assumption that the group is monophyletic. The studies of McLellan (1977) and Casinos (1978; 1981) included taxa which properly belong to the Gadoidei. Indications from jaw-opercular linkages and muscle insertions are that gadoids employ a different feeding mechanism from that of macroroids. The extrapolation of data gleaned from functional studies of acanthopterygian fishes to 'paracanthopterygians' is a flawed approach.

Ecological

Hypotheses of trophic strategies have also suffered by the tacit assumption of macroroid monophyly. The ecological and evolutionary scenarios of McLellan (1977) and Casinos (1978) must be reassessed in the light of the revised classification of macroroids and gadoids (Howes, 1988; Howes & Crimmen, in prep.).

That the monophyly of a group so seemingly highly characterised as the Macroroidae should be questioned is a warning that functional and ecological hypotheses must be used guardedly and are valid only for groups whose monophyly is well corroborated.

According to Lauder's (1981) 'decoupling hypothesis' there is a phylogenetic increase in the number of biomechanical components and their pathways. Thus the derived sister taxon of a group

displays greater diversity and 'constructional flexibility' than its plesiomorphic sister taxon. The Gadoidei are hypothesised to be the derived sister group of the Macrouroidei (see Howes, 1988), and as such Lauder's hypothesis is borne out (in part) since the macrouroids lack what might be the more manipulative functions of the upper jaws possessed by gadoids. There is also a more complex arrangement of the hyoid and ventral gill-arch musculature in gadoids, although it is arguable whether a greater range of function is achieved (see p. 54). Only a complete comparative functional analysis of feeding mechanisms of taxa in the two groups will support Lauder's claim.

The intrarelationships of the morphologically diverse genera assigned to the Macrourinae have yet to be worked out cladistically. Myological characters have not been rewarding in this regard, and synapomorphies must be sought in other soft-anatomical (particularly in the structure of the light organs) and skeletal features.

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